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# FACTORS IN THE INCEPTION AND DEVELOPMENT OF FUSARIUM ROT IN STORED POTATOES

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CONTENTS

| | Page |
|---|---|
| Introduction | 1 |
| Sources of Fusarium tuber rot | 1 |
| Economic importance of Fusarium rot in market potatoes | 2 |
| Experimental data | 6 |
| Methods and materials | 6 |
| Thermal relations of Fusarium in artificial cultures and in tuber pathogenicity | 8 |
| Relation of humidity to infection | 10 |
| Relation of infection to kind of injury and its healing | 17 |
| Effect of suberization and wound-periderm formation on infection | 20 |
| Experimental data—Continued | Page |
| Effect of varietal difference | 25 |
| Relation of relative humidity at higher temperatures to infection | 26 |
| Discussion of results | 29 |
| Prestorage handling methods to prevent infection through harvesting injuries | 29 |
| Storage methods to insure keeping quality and prevent rot | 31 |
| Conclusions | 31 |
| Summary | 32 |
| Literature cited | 34 |

## INTRODUCTION

### SOURCES OF FUSARIUM TUBER ROT

Potato tuber rots caused by one or another species of Fusarium originate in two principal ways: (1) By direct penetration during the growth of the tuber, either from a diseased parent plant through the stolon or from the soil through lenticels and eyes; (2) after growth is completed, and usually during or after harvest, by secondary extension of a lesion in which the primary injury may have been caused mechanically, by extremes of temperature, by chemicals, or by another parasite. In general, these divisions correspond to the so-called field rots and storage rots, and the groups of organisms

[1] Facilities for carrying on a comprehensive study of the problem of Fusarium tuber rots were offered by the Marble Laboratory (Inc.), of Canton, Pa. This laboratory is uniquely equipped for such an investigation. It affords storage chambers of size and construction typical of commercial warehouses and far more representative of practical conditions than ordinary laboratory equipment. Not only is automatic equipment available for the simultaneous control of temperature, humidity, and rate of air exchange, but this is supplemented by hourly inspection, and manual adjustment when necessary, throughout the day during an experiment of any desired length. From September, 1925, to December, 1926, the facilities of the laboratory were placed unreservedly at the disposal of the writers, and it is in fact due to the availability of such facilities that this investigation has been carried out. The Marble Laboratory also purchased the potatoes used in the experiments, or provided land on the laboratory farm for growing them. Special acknowledgment is due to L. M. Marble for the benefit which his practical storage experience has conferred on the plans for the experiment and the interpretations growing out of the results.

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which occupy the causative rôles, respectively, to high and low temperature forms. The correspondence is not exact, as infections which originate in the field may continue in storage at lower temperature; and though the widespread reintroduction of storage-rot Fusaria into the soil with infected seed usually results only in destructive competition between fungus and sprout for the substance of the seed piece, the organisms of this group are able on occasion to cause stem rot and perhaps root rot of growing plants.

Among the six species of outstanding importance, a rough partition into a field-rot group, including *Fusarium oxysporum*, *F. radicicola*, and *F. eumartii*, and a storage-rot group, including *F. coeruleum*, *F. sulphureum*, and *F. trichothecioides*, usually is made. *F. oxysporum* is reputed to be the principal cause of potato wilt throughout the southern part of the late potato-producing area of the United States, but it is also a very active parenchyma destroyer in regions farther south, and is responsible for much loss in transit. *F. radicicola* is best known in various ways as a tuber-rotting parasite, but it may cause stem rot and vascular discoloration (*22*)[2]. *F. eumartii* in Pennsylvania is chiefly recognized as the cause of a stem-end rot at harvest which may develop into a typical dry rot under certain storage conditions, but in Nebraska emphasis is placed on its capacity as a root parasite to cause wilt (*7*). *F. trichothecioides*, found by Pratt (*23*) to be strictly a storage parasite apparently incapable of infecting growing plants though variously inoculated into them, was reported by Link (*11*) to be able to attack any subterranean part of the living plant; however, only the mature tuber is generally susceptible. *F. sulphureum* and *F. coeruleum* in nature seem invariably associated with decay of tubers, including those planted as seed, but are able to produce only very minor lesions on stems and stolons when growing plants are inoculated.

A comprehensive treatment of the relation of species of Fusarium to potato diseases must recognize the interrelation of plant and tuber, field and storage, infections. Considerable experience with potato-pathogenic Fusaria, however, supports the segregation into these two classes in so far as the species of principal importance are concerned. This bulletin deals with the Fusarium tuber rots that typically occur, with considerable detriment, in the late-potato crop of the United States at any time after placing in low-temperature storage, that is to say, mainly with *Fusarium coeruleum F. sulphureum*, and *F. trichothecioides*, but with supplementary data on *F. oxysporum*, *F. radicicola*, and *F. eumartii*.

### ECONOMIC IMPORTANCE OF FUSARIUM ROT IN MARKET POTATOES

Fusarium rot is more or less generally present in unsound potatoes in terminal markets. This is the basis for the frequently quoted statement (*12*) that "taking the potato crop as a whole, Fusarium tuber rot causes greater losses in storage than all other diseases combined." Not all such rot, however, is originally and primarily due to Fusarium; consideration must be given to the frequently secondary character of Fusarium infection. The principal factors that predispose to Fusarium rot may be classified as (1) wounds, by which is meant any injury in which the periderm (skin) is ruptured or underlying tissues are crushed; (2) extremes of temperature, of which low temperature is the more frequent source of injury to main-crop pota-

[2] Reference is made by italic numbers in parentheses to "Literature cited," p. 34.

toes; (3) late blight tuber rot, caused by *Phytophthora infestans;* (4) miscellaneous injuries due to salt and other chemicals, surface pitting and internal breakdown (black heart) due to respiratory disturbances; (5) field infection by Fusarium through natural openings. The importance of the last factor has not yet been determined; both Wilcox and others (*27*) and Pratt (*23*) reported entirely negative results from attempts to infect potatoes through the unbroken skin with *F. trichothecioides*, but Pethybridge (*19*) found *F. coeruleum* able to infect tubers through lenticels, eyes, and young sprouts, and Bisby (*3*) reported infection, probably through lenticels, with *F. sulphureum.* All these authors testify to the predominant importance of infection through wounds.

Table 1 shows the number of times each of the conditions listed above is associated with a record of Fusarium rot in the reports of inspectors of the office of market inspection of fruits and vegetables of the Bureau of Agricultural Economics, United States Department of Agriculture, in the last five years.[3] The last column of the table, however, does not represent field infection through natural openings; this may have been the source of infection, but the report only indicates that no defects other than Fusarium rot were observed.

TABLE 1.—*Incidence of various predisposing conditions in relation to Fusarium decay, showing the number of times each condition was reported in stated years*

| Year | Fusarium decay (carloads) | Wounds | Frost injury | Late blight | Miscellaneous injuries | No defects |
|---|---|---|---|---|---|---|
| 1922 | 489 | 287 | 158 | 47 | 78 | 62 |
| 1923 | 1,722 | 1,483 | 613 | 173 | 80 | 114 |
| 1924 | 1,038 | 758 | 302 | 88 | 86 | 64 |
| 1925 | 1,360 | 946 | 305 | 210 | 84 | 90 |
| 1926 | 1,538 | 993 | 243 | 375 | 808 | 423 |

In the different years the number of concomitant records of injuries conspicuous enough to report is 60 to 85 per cent of the number of records of decay, but in no instance does the occurrence of any other one condition exceed a proportion of 35 per cent. This would indicate that wounds are the source of Fusarium decay about twice as often as any other factor. Pethybridge and others (*20, 21*) state that 80 per cent or more of a dry rot of potatoes in Ireland, later determined to be due to *Fusarium coeruleum*, was traceable to wounds. Pratt (*23*) studied experimentally the relation of wounds and soil contamination to infection by *F. trichothecioides* and concluded that potatoes in storage are attacked only through injuries.

An idea of the economic importance of Fusarium tuber rots may be gained from the market-inspection records. In most of the inspection reports an attempt is made to estimate the percentage of loss due to Fusarium decay, this being based on actual weight and usually on examination of at least eight sacks in each car inspected. In Table 2 the average percentage of Fusarium decay found in market potatoes is shown for 18 States producing a late-crop surplus for the last five years. When the inspection report expressed a range

[3] The data in Tables 1 to 4 were compiled from the records of inspections made by the farm products inspection service in response to requests by shippers, carriers, or consignees. A request for inspection usually implies a question on the part of one or another of these parties as to the condition of a shipment. Since the presence of decay is only one of the factors affecting the grade of potatoes and requests for inspection are made frequently in regard to some other condition, it is believed that the records are representative of all the potatoes entering inspection markets and in a general way of the entire main crop of the country. About 13,000 records were examined, each representing one carload assumed to be 600 bushels.

of percentages, a figure slightly lower than the mean value was selected, so the average percentage arrived at is uniformly conservative. It appears that between 3 and 4 per cent is the average country-wide loss due to Fusarium in potatoes reaching terminal markets, but this does not express the total loss from this cause, as the stock for which this figure is computed in most cases had been graded once or twice previously, and more or less decay was thus eliminated. It is not unlikely that 5 to 10 per cent more nearly represents the total loss due to Fusarium in late potatoes. The summaries of losses in potatoes caused by plant diseases as compiled by the Plant Disease Survey of the Bureau of Plant Industry do not take account of dry rot in storage, but in individual State records this loss is estimated to range from less than 1 to 25 per cent. Morris and Nutting (*16*) state that in Montana the loss in 1917—a representative year—was 3 per cent from dry rot and 4 per cent from wilt.

TABLE 2.—*Average percentage of Fusarium decay in market potatoes from 18 States producing a late-crop surplus, as shown by inspection records*

| State | 1922 | 1923 | 1924 | 1925 | 1926 | Five-year average |
|---|---|---|---|---|---|---|
| California | 4.00 | 12.00 | ---------- | 1.00 | 14.00 | 7.75 |
| Colorado | 4.64 | 3.50 | 2.73 | 2.69 | 2.63 | 3.30 |
| Idaho | 4.06 | 4.50 | 7.70 | 4.09 | 6.44 | 5.36 |
| Maine | 2.58 | 3.19 | 2.93 | 3.10 | 2.41 | 2.84 |
| Michigan | 1.86 | 2.47 | 2.21 | 3.10 | 2.51 | 2.43 |
| Minnesota | 2.40 | 3.50 | 3.63 | 3.56 | 2.78 | 3.17 |
| Montana | 1.72 | 5.84 | 12.00 | 3.00 | 4.70 | 5.45 |
| Nebraska | 5.00 | 4.91 | 6.16 | 4.83 | 2.33 | 4.64 |
| New York | 3.44 | 1.91 | 1.88 | 3.41 | 3.17 | 2.76 |
| North Dakota | 2.55 | 3.38 | 2.40 | 3.47 | 3.17 | 2.99 |
| Oregon | 5.50 | 5.66 | 3.64 | 1.00 | 2.84 | 3.73 |
| Pennsylvania | 2.54 | 4.15 | 4.33 | 3.91 | 2.77 | 3.54 |
| South Dakota | 1.00 | 1.50 | 2.00 | 1.50 | ---------- | 1.50 |
| Utah | 1.00 | 4.20 | ---------- | ---------- | 5.00 | 3.40 |
| Vermont | ---------- | 4.00 | ---------- | ---------- | 4.50 | 4.25 |
| Washington | ---------- | 3.90 | 3.48 | ---------- | 4.49 | 3.96 |
| Wisconsin | 2.35 | 1.82 | 3.32 | 4.45 | 2.74 | 2.94 |
| Wyoming | 3.37 | 4.36 | 1.00 | ---------- | 4.50 | 3.30 |
| Average | 3.00 | 4.15 | 3.96 | 3.08 | 4.17 | 3.74 |

TABLE 3.—*Calculated loss in export late potatoes from Fusarium decay based on the loss indicated by market inspections*

| State | Five-year average, 1922–1926 | | | |
|---|---|---|---|---|
| | Shipments | Fusarium decay | Affected by decay | |
| | *Carloads* | *Per cent* | *Carloads* | *Bushels* |
| California | 6,930 | 7.75 | 537 | 322,000 |
| Colorado | 14,948 | 3.30 | 493 | 296,000 |
| Idaho | 15,787 | 5.36 | 846 | 518,000 |
| Maine | 36,572 | 2.84 | 1,038 | 623,000 |
| Michigan | 17,638 | 2.43 | 428 | 257,000 |
| Minnesota | 28,507 | 3.17 | 903 | 542,000 |
| Montana | 1,040 | 5.45 | 56 | 34,000 |
| Nebraska | 4,312 | 4.64 | 200 | 120,000 |
| New York | 17,092 | 2.76 | 471 | 283,000 |
| North Dakota | 6,941 | 2.99 | 207 | 124,000 |
| Oregon | 1,718 | 3.73 | 64 | 38,000 |
| Pennsylvania | 4,440 | 3.54 | 157 | 94,000 |
| South Dakota | 2,011 | 1.50 | 30 | 18,000 |
| Utah | 1,207 | 3.40 | 41 | 25,000 |
| Vermont | 180 | 4.25 | 7 | 4,000 |
| Washington | 7,137 | 3.96 | 282 | 169,000 |
| Wisconsin | 17,026 | 2.94 | 500 | 300,000 |
| Wyoming | 848 | 3.30 | 28 | 17,000 |
| Total | ---------- | ---------- | ---------- | 3,784,000 |

Table 3 shows the five-year average of car-lot shipments from the same 18 States for the period 1922–1926 and translates the percentage of Fusarium infection into losses from Fusarium decay (in carloads and bushels), assuming the same percentage of infection to apply throughout. It should be borne in mind that the loss as thus stated is in reduced salability and not in all cases in stock destroyed outright.

The extent to which it is justifiable to project the amount of Fusarium decay actually determined in market inspections to the amount occurring in that portion of the entire crop that is shipped by rail may be gathered from Table 4, which shows the total number of inspection reports examined in relation to the five-year average of carload shipments from a group of 17 States.

TABLE 4.—*Inspections of late-crop potatoes, by years, compared with five-year average shipments in 17 States, 1922–1926*

| State | Inspected, by years (carloads) | | | | | Shipments, five-year average (carloads) |
|---|---|---|---|---|---|---|
| | 1922 | 1923 | 1924 | 1925 | 1926 | |
| California | 11 | 16 | 1 | 5 | 7 | 6,930 |
| Colorado | 145 | 235 | 310 | 184 | 286 | 14,948 |
| Idaho | 98 | 307 | 89 | 96 | 226 | 15,787 |
| Maine | 103 | 430 | 590 | 1,154 | 1,225 | 36,572 |
| Michigan | 210 | 682 | 408 | 306 | 362 | 17,638 |
| Minnesota | 335 | 684 | 380 | 408 | 327 | 28,507 |
| Montana | 28 | 38 | 10 | 4 | 23 | 1,040 |
| New York | 118 | 256 | 514 | 287 | 196 | 17,092 |
| North Dakota | 46 | 116 | 31 | 61 | 55 | 6,941 |
| Oregon | 3 | 35 | 65 | 9 | 24 | 1,718 |
| Pennsylvania | 19 | 26 | 36 | 29 | 22 | 4,440 |
| South Dakota | 8 | 18 | 2 | 5 | 0 | 2,011 |
| Utah | 13 | 17 | 2 | 5 | 20 | 1,207 |
| Vermont | 0 | 2 | 0 | 0 | 6 | 180 |
| Washington | 0 | 26 | 88 | 16 | 83 | 7,137 |
| Wisconsin | 105 | 245 | 92 | 162 | 186 | 17,026 |
| Wyoming | 4 | 15 | 4 | 16 | 14 | 848 |

The facts emerging from this survey, that more than 3,000,000 bushels of potatoes annually are affected with Fusarium rot, after having incurred their proportion of the costs of production, storage, and transportation, and that two-thirds or more of this decay originates in handling injuries, justify considerable effort to determine under what conditions infection of wounds takes place and how it may be prevented. Furthermore, the amount of loss in storage locally is sometimes much greater, becoming even the limiting factor in profitable potato production. In the storage house of the Potter County Potato Growers' Association at Coudersport, Pa., from 30 to 70 per cent of the crop stored in different years was affected by rot (*14*). The warehouse was new and had been constructed in accordance with approved principles. Part of the difficulty was traced to bulk storage of large masses of potatoes and to inadequate ventilation, but even when, in 1924, a forced-ventilation system was installed, the temperature held at about 3.5° C., and the stock stored in bags, shrinkage due to rot still amounted to more than 20 per cent (*18*).

Conclusions regarding the relation of temperature and humidity to Fusarium tuber rot heretofore have depended mainly on the work of Goss (*6*), who studied the influence of these factors on tuber infection by *Fusarium oxysporum*, *F. radicicola*, and *F. trichothecioides*, and

on data obtained with less precise control of conditions by Link (*11*), Pratt (*23*), and Bisby (*3*). Goss concluded that only *F. trichothecioides* was able to initiate rot at 5° C., and only in a saturated atmosphere. At somewhat higher temperatures the extent of rot produced by each species corresponded roughly to the relative humidity, very low humidity suppressing infection entirely. At 25° C. infection occurred at the lowest humidity employed, but the amount of rot increased with the percentage of saturation. This would indicate that humidity is of the greatest influence at low temperature, though physiological dryness, as measured by the saturation deficit, is greater with the same relative humidity as the temperature increases.

Since the species studied by Goss are not those of importance in eastern storage, where experience shows that rotting may occur below 5° C., it was considered advisable to reinvestigate the problem of Fusarium tuber rots, taking into consideration the relation of environmental factors and handling methods in storage and the behavior of different varieties of potatoes and different species of Fusarium.

## EXPERIMENTAL DATA

### METHODS AND MATERIALS

#### CONSTRUCTION AND OPERATION OF THE STORAGE CHAMBERS

The general features of construction of the storage house have been described elsewhere (*18*). The experimental chambers were seven in number; in size, 11 by 11, or 7 by 9, and 10 feet high. All were equipped with slatted false floors under which the ventilating outlets were distributed. Air, properly conditioned as to temperature and moisture content by circulation through brine humidifiers or moistened further by injection of steam, was circulated slowly through the chambers. Except where a definite rate of air exchange was desired, the circulation was only rapid enough to maintain the desired conditions and was not measured. The experimental lots of tubers were placed in clean 4-quart till baskets, which were arranged in tiers on shelves or stacked on the floor so that free circulation through and around them was possible. At first duplicate baskets were kept at two different heights from the floor, but no difference in temperature or humidity could be detected in the two positions, and no influence on the results was evident. The chambers were totally dark and were disturbed as little as possible, most inspections and adjustments being made from the outside. Continuous records of temperature and humidity were kept on Friez hygrothermographs. Several records are reproduced in Figure 1 to show the average character of control. In some weeks the control was much closer than that here illustrated, and at no time during 10 months of operation did any factor vary from the desired standard by an amount exceeding half the difference between successive intervals.

#### SOURCE AND TREATMENT OF EXPERIMENTAL POTATOES

In 1925, 100 bushels of each of the varieties White Rural, Russet Rural, Green Mountain, and Spaulding Rose, all produced on one farm, were placed in crates in the field and hauled directly to the laboratory, where they were put in cellar storage without further handling. The next year the same varieties, together with Irish Cobbler and Triumph, were grown in one plot on the laboratory

farm. In this way stocks were obtained that accurately reflected differences due to variety and not to different cultural conditions under which they were produced. Likewise the careful and minimum handling and the favorable storage conditions resulted in stock that was initially free from mechanical injuries and that kept practically dormant and entirely free from rot throughout the experiments.

Before their use in inoculation experiments, the tubers were scrubbed, treated in 0.1 per cent mercuric chloride for 15 minutes, rinsed, and dried. In certain experiments different forms of mechanical injury, such as cutting, bruising, and skinning, were inflicted on whole tubers. As a standard form of injury when environmental factors were under study, large tubers were halved or quartered, and small ones used whole, and a tangential slice, usually about 1 cm.

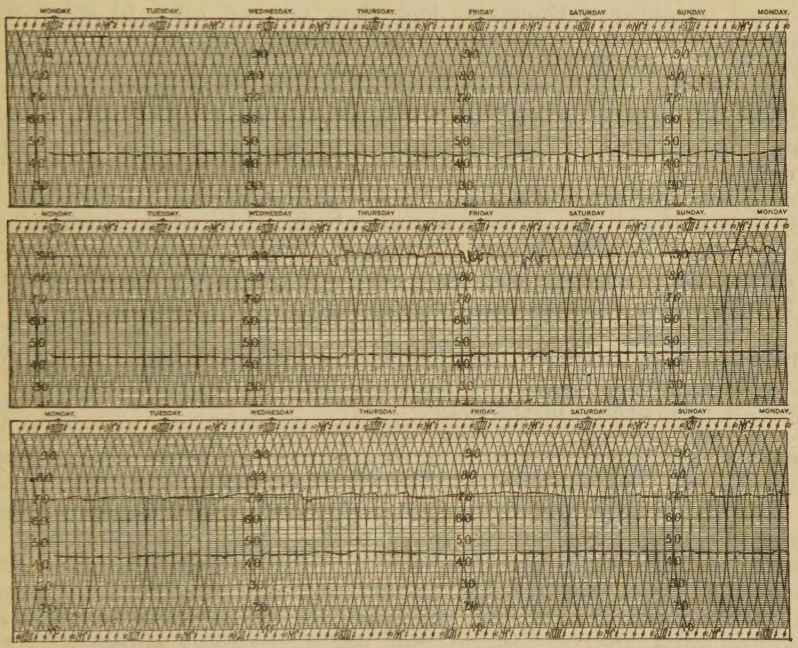



FIG. 1.—Samples of hygrothermograph records, showing the efficiency of the temperature and humidity control.

thick, removed with a sharp knife which had been dipped in alcohol and flamed. Heating to an extent that would cause burning and interfere with the healing of the injury was avoided. The cut surface was inoculated at once, unless the effect of an interval following cutting was under study. The tubers were then placed in a single layer, with the inoculated surface up, in till baskets and immediately removed to a controlled environment. Each set was inoculated in duplicate, one lot being placed at once under the permanent storage conditions, the other in a nearly saturated atmosphere at the same temperature, whence it was removed after 48 hours and placed with the first. Five or ten tubers constituted the experimental unit; if 10, usually only half the lot was cut for examination at the end of the first storage interval, and the remainder was left for an additional period to determine whether decay would continue or had been checked after some initial progress.

### SOURCE OF CULTURES AND METHODS OF INOCULATION

From the writers' herbarium of potato Fusaria, cultures were selected which had been under study for some time and were known to be typical of each included species in their growth characteristics and effects on potatoes. They were plated several times to insure freedom from contaminating organisms, but were not pure lined in the sense of being derived from a single spore or hyphal tip. For inoculating, cultures were multiplied in small flasks of oatmeal agar, or were transplanted to Petri dishes of synthetic potato agar and allowed to cover the medium. When mycelium was used as inoculum, a small mass of the medium was included. The use of Petri dishes for multiplying cultures permitted approximate standardization of the quantity of the medium thus included, as the plates could be poured of uniform thickness and then marked off into squares of approximately the same size. The favorable effect on infection of including some of the culture medium together with mycelium as inoculum has been shown by Wilcox and others (*27*). When the plane cut-surface type of wound was employed, the inoculum was laid flat upon it. The inoculum adhered firmly, and no further puncture or cut was made.

Spore suspensions also were utilized in comparison with mycelium for inoculation. These were not standardized as to their spore content, but were made moderately dense. For use they were placed in Petri dishes to a depth of about 5 mm. and the tubers were inoculated by dipping the cut surface momentarily.

For inoculating different forms of mechanical injuries, cultures in loam and compost were tested. Such material was inserted in cuts or rubbed into bruised and skinned areas to simulate infection of wounds as it occurs in the field.

### THERMAL RELATIONS OF FUSARIUM IN ARTIFICIAL CULTURES AND IN TUBER PATHOGENICITY

The historical aspects of the thermal relations of Fusarium species in artificial cultures and in tuber pathogenicity were reviewed by Goss (*6*). The work of Carpenter (*4*), Wilcox, Link and Pool (*27*), Link (*11*), Pratt (*23*), Bisby (*3*), and Goss (*6*) showed that the several species capable of causing tuber rots vary in their temperature requirements, that in general they are increasingly active with rise of temperature corresponding to their growth rate in artificial cultures, that *Fusarium oxysporum* and *F. eumartii* cause little or no rot below 10° C. and *F. radicicola* little or none below 8.5°, but that *F. trichothecioides* and *F. sulphureum* are not entirely checked by low temperature until about 2° is reached. Two supplementary questions are raised by these authors, but not definitely settled: (1) Do similar thermal relations govern the production or extension of mycelium in artificial media and the advance of decay in tubers? (2) Are the thermal relations of infection the same as those which influence the progress of decay?

With respect to the first, Goss (*6*) observed that the use of a synthetic medium and of dry weight of mycelium as a criterion of growth led to results similar to those reported by Edson and Shapovalov (*5*) and found by himself, when potato agar was employed and radial extension measured. For example, the minimum, optimum, and maximum temperatures for growth of *Fusarium trichothecioides*

were found to be 5°, 25°, and 30° C. When a potato-extract medium was used, the optimum was found to be 15° to 20°. A similar shift of the optimum with change of medium might account for the circumstance reported by Wilcox and others (*27*) that, contrary to the usual temperature effect, the progress of rot due to this organism is greater at 8° to 10° than at 24° to 27°.

Evidence bearing on the second question also is presented in the work of the authors cited. Pratt found that tubers which had been inoculated with *Fusarium trichothecioides* did not decay when the temperature of incubation averaged 0.8° C., but that slight to considerable decay occurred respectively at 4.2° and 7.6°. According to Bisby (*3*), *F. sulphureum* is able to make a little growth on artificial media at 1.1° to 1.7° and also to cause a slight amount of rot at the same temperature. Edson and Shapovalov (*5*) observed that germination, but no visible growth, of *F. trichothecioides* occurred on agar plates in seven days at 5°, whereas *F. sulphureum* produced visible growth in two weeks at 1°. It appears that these two species can initiate a tuber rot at the lowest temperature at which germination or growth in artificial media occurs or decay, once started, continues. That the same relation does not hold at higher temperatures will be evident from the results herein described.

Preliminary tests were made to determine the temperature range for infection of potato tubers by the several species of Fusarium previously named. Inoculations were made by placing a square about 5 mm. in diameter from an agar culture on a freshly cut tuber which was placed in a loosely covered dry dish in an incubator. Experience with this method of inoculation had shown that the use of a moist chamber has no particular advantage. Although different varieties of potatoes were used, the tests were on a scale too small to make such differences significant. The criterion of infection in this and subsequent experiments is depth of penetration. (Table 5.)

TABLE 5.—*Effect of temperature on tuber infection of potato varieties by six species of Fusarium.*

[The figures express total penetration in millimeters from 2 inoculations]

| Species of Fusarium and variety of potato | Temperature (° C.) | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| | 0 | 5 | 10 | 15 | 20 | 25 | 30 | 35 |
| F. trichothecioides: | | | | | | | | |
| White Rural, old | 0 | 2.5 | 7 | 26 | 13 | 4.0 | 0 | ------ |
| Raleigh, old | 0 | 22.0 | 32 | 32 | 3 | 2.5 | 1.5 | ------ |
| Irish Cobbler, new | ------ | 0 | 10 | 12 | 18 | 10. | 0 | ------ |
| F. sambucinum: | | | | | | | | |
| Raleigh, old | 1.5 | 7.0 | 20 | 5 | 17 | 4.0 | 1 | ------ |
| F. sulphureum: | | | | | | | | |
| White Rural, old | 5.0 | 12.5 | 14 | 40 | 15 | 34.0 | 1 | ------ |
| F. coeruleum: | | | | | | | | |
| White Rural, old | 4.0 | 14.0 | 12 | 14 | 10 | 3.0 | 0 | ------ |
| Irish Cobbler, new | ------ | 10.0 | 16 | 30 | 40 | 0 | 0 | ------ |
| F. eumartii: | | | | | | | | |
| Irish Cobbler, new | ------ | 0 | 1 | 4 | 26 | 10.0 | 30 | 0 |
| F. oxysporum: | | | | | | | | |
| Irish Cobbler, new | ------ | ------ | 0 | 0 | 0 | 4.0 | 100 | 60 |

The data in Table 5 indicate that so far as the establishment of infection is concerned, the optimum temperature for the typical storage-rot organisms is about midway between 10° and 20° C., and

that two species are able to cause rot at 0°. It is worthy of note that the typical storage-rot species were practically unable to infect at 30°, and found even 25° less favorable than lower temperatures, though it is a matter of common observation that dry rot is generally accelerated by removal from cold storage to a warm room. Thus, when 20 tubers were inoculated with *Fusarium coeruleum* and 10 held at 12° and 10 at 25° C., the average penetration at each temperature was 6.5 mm. per tuber in 30 days. When 10 tubers which had been held at 10° for 30 days, until decay was well established, were transferred to 25° for a similar period, the decay averaged over 20 mm. per tuber.

A hypothesis may now be framed to account for the behavior of these Fusaria in the infection of tubers: (1) Increase of temperature, within limits which vary with different species, has the same (favorable) effect on the progress of an established rot as on the growth of mycelium in artificial cultures; (2) whereas low temperature does not retard infection more than it does the growth of mycelium, high temperature, though favorable for growth, may sometimes be unfavorable for infection. This will be reverted to later. The influence of the second principal environmental factor will next be taken up.

### RELATION OF HUMIDITY TO INFECTION

Besides the work of Goss (*6*), whose results on this factor have been reviewed, other incidental experiments on the relation of humidity to tuber infection have been reported. Weld and Wollenweber (*26*) stated that penetration by *Fusarium trichothecioides* was deeper in tubers incubated in a dry chamber than in those kept in a moist chamber when the temperature was 10° to 12° C. In the experimental inoculations reported by Wilcox and others (*27*), the humidity in the incubating dishes was modified by the use of water or a desiccating agent. At 8° to 10° penetration was greater at the higher humidity. At 27° no difference due to humidity appeared. Bisby (*3*), employing similar methods, found that infection could occur under dry conditions through deep wounds. Pratt (*23*) concluded that the drier the atmosphere in storage the less will be the loss from powdery dry rot, but in the experiment on which this view is based the effects of temperature and humidity were not segregated. None of these authors report measurements of the humidity in their experiments.

Goss adopted relative humidity as a measure of the moisture content of the atmosphere and employed the same four relative humidities at three different temperatures. If the effect of atmospheric moisture on infection results from the equilibrium established with the water content of the inoculum or the host tissues, it is evident that the use of the same relative humidities at different temperatures does not impose uniform conditions on infection, since the evaporating power of the air is, for example, about three times as great for the same relative humidity at 25° as at 9° C. However, Goss's results indicated apparently an even greater influence of humidity when the temperature was near the minimum for infection than when it approached the optimum, which may be an example of the compensatory effect of the two factors. His work also showed that atypical infection results from the attempt to control humidity within a closed space, as, for example, in a desiccator by the use of sulphuric

acid of a calculated density, and that it is due to the lack of air. Circulating air was employed in his later experiments.

In the present work preliminary tests confirmed the unfavorable effect of confining tubers in a desiccator, but emphasized another difficulty in this method of regulating humidity, namely, the effect of slight fluctuations in the temperature or the existence of a temperature gradient which unequally affects different parts of the desiccator. It was found that the ordinary fluctuations of the laboratory temperature sufficed to permit temporary and periodic condensation in a desiccator containing 500 to 700 gm. of tubers and 500 c. c. of sulphuric acid of a density calculated to maintain 50 per cent humidity at 25° C. It also developed that when as few as 10 freshly cut tubers were inclosed in a 5-liter desiccator which was held in a room maintained at 6.5°, though with a certain amount of stratification due to absence of air circulation, local condensation on the side next to a cold wall occurred even though air at 50 per cent saturation was passed through at the rate of one change an hour.

Such defects of humidity control did not of course occur in the work carried on in the large storage chambers previously described, where the volume of inoculated tubers was always insignificant in relation to that of the chamber. They are mentioned as a caution in experimentation in humidity control with apparatus of limited capacity.

TABLE 6.—*Relation of relative humidity at 6.7° C. to infection of four varieties of potatoes by Fusarium trichothecioides and F. coeruleum*

[Data in millimeters, showing the total penetration of five tubers. The compound designations 98–90 98–80, and 98–70 mean that incubation was at the higher humidity for 2 days, thereafter at the lower]

| Variety and humidity | Infection by Fusarium trichothecioides | | | | | Infection by Fusarium coeruleum | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | Early storage Oct. 1 to— | | Middle storage Oct. 29, 1925, to— | | Late storage, Mar. 30 to May 6, 1926, 1 month | Early storage Oct. 1 to— | | Middle storage, Oct. 29, 1925, to— | | Late storage, Mar. 30 to May 6, 1926, 1 month |
| | Oct. 28, 1925, 1 month | Dec. 15, 1925, 3 months | Dec. 15, 1925, 1 month | Feb. 9, 1926, 3 months | | Oct. 28, 1925, 1 month | Dec. 15, 1925, 3 months | Dec. 15, 1925, 1 month | Feb. 9, 1926, 3 months | |
| Russet Rural: | | | | | | | | | | |
| 98 per cent | 15.0 | 28.0 | 14 | 56 | 11 | 10.0 | 66.0 | -------- | 75 | 14.0 |
| 98–90 per cent | 16.0 | 16.0 | 11 | 13 | -------- | 15.0 | 39.0 | 36 | 39 | -------- |
| 98–80 per cent | 14.0 | 23.0 | 14 | 33 | -------- | 9.0 | 46.0 | 34 | 62 | -------- |
| 98–70 per cent | 13.0 | 24.0 | 18 | 28 | -------- | 10.0 | 41.0 | 34 | 55 | -------- |
| 90 per cent | 12.5 | 31.0 | 16 | 14 | 11 | 17.5 | 68.0 | 27 | -------- | 23.0 |
| 80 per cent | 12.0 | 17.0 | 25 | 20 | 10 | 19.0 | 42.0 | 19 | -------- | 24.0 |
| 70 per cent | 14.0 | 16.0 | 26 | 19 | 8 | 11.0 | 60.0 | 20 | -------- | 6.5 |
| White Rural: | | | | | | | | | | |
| 98 per cent | 15.0 | 38.0 | 14 | 77 | 12 | 13.0 | 40.0 | -------- | 45 | 18.0 |
| 98–90 per cent | 15.0 | 19.0 | 19 | 17 | -------- | 22.5 | 41.0 | 35 | 53 | -------- |
| 98–80 per cent | 14.0 | 17.0 | 12 | 13 | -------- | 10.0 | 40.0 | 40 | 61 | -------- |
| 98–70 per cent | 14.0 | 22.0 | 15 | 23 | -------- | 10.0 | 46.0 | 38 | 84 | -------- |
| 90 per cent | 15.0 | 14.0 | 50 | 116 | 8 | 3.5 | 39.0 | 19 | -------- | 24.0 |
| 80 per cent | 9.5 | 16.0 | 43 | 60 | 8 | 2.5 | 60.0 | 36 | -------- | 8.0 |
| 70 per cent | 12.5 | 13.0 | 21 | 45 | 9 | 4.5 | 55.0 | 28 | -------- | 17.0 |
| Green Mountain: | | | | | | | | | | |
| 98 per cent | 14.0 | 35.0 | 12 | 12 | 8 | 13.0 | 60.0 | 34 | 80 | 14.0 |
| 98–90 per cent | 17.0 | 16.0 | 15 | 13 | -------- | 19.0 | 51.0 | 41 | 66 | -------- |
| 98–80 per cent | 12.0 | 20.0 | 16 | 17 | -------- | 4.5 | 38.0 | 31 | 64 | -------- |
| 98–70 per cent | 15.0 | 18.0 | 51 | 51 | -------- | 11.0 | 38.0 | 44 | 93 | -------- |
| 90 per cent | 16.0 | 12.0 | 13 | 15 | 6 | 2.5 | 30.0 | 36 | 68 | 13.0 |
| 80 per cent | 12.0 | 28.0 | 21 | 20 | 13 | 4.0 | 55.0 | 46 | 78 | 8.0 |
| 70 per cent | 13.0 | 28.0 | 37 | 64 | 11 | 4.0 | 55.0 | 29 | 60 | 10.0 |
| Spaulding Rose: | | | | | | | | | | |
| 98 per cent | 15.0 | 15.0 | 15 | 14 | 7 | 10.0 | 10.0 | 26 | -------- | 19.0 |
| 98–90 per cent | 12.5 | 12.5 | 12 | 12 | -------- | 20.0 | 17.5 | 38 | 71 | -------- |
| 98–80 per cent | 20.0 | 42.0 | 23 | 67 | -------- | 12.5 | 38.0 | 33 | 86 | -------- |
| 98–70 per cent | 13.0 | 41.0 | 50 | 90 | -------- | 13.0 | 40.0 | 44 | 50 | -------- |
| 90 per cent | 12.0 | 13.0 | 15 | 19 | 9 | 22.5 | 16.0 | 30 | -------- | 12.5 |
| 80 per cent | 17.5 | 28.0 | 65 | 78 | 9 | 7.5 | 47.0 | 28 | -------- | 4.5 |
| 70 per cent | 16.0 | 41.0 | 36 | 100 | 22 | 8.0 | 46.0 | 28 | -------- | 8.0 |

In Table 6 data are summarized from all the experiments on the relation of humidity to infection in which the same form of inoculation with mycelium applied to a freshly cut surface was followed. The temperature 6.7° C. (44° F.) was selected as representative of good cellar-storage conditions and employed throughout the experiments on the relation of humidity to infection. The storage term, October 1 to March 30, is divided into three periods, early, middle, and late, to show whether a difference exists in susceptibility to rotting depending on the age in storage. Of the four varieties, only Spaulding Rose showed the beginning of sprout activity when the last experiment was begun (March 30), but sprouting occurred in Green Mountain and very slightly in White Rural and Russet Rural before its close. The intervals between inoculations and readings were not quite uniform, but corresponded roughly to the designations "1 month" and "3 months" employed in the table. Where a second interval is stated, it means that five tubers of each lot were examined one month after inoculation and five others about two months later. Every inoculated tuber became infected. As a convenient measure of infection, the total penetration in five tubers was adopted.

It appears that at this temperature infection is not positively correlated with relative humidity within the range of 70 per cent to near saturation. There is some indication in Spaulding Rose and Green Mountain that penetration is greater at the lower humidities, whereas at 90 to 98 per cent effective healing takes place, as is indicated by a penetration no greater in three months than in one.

It might be thought that the absence of any apparent relation between humidity and infection is due to the establishment of a stratum of high moisture content over the freshly cut sap-exuding surface during the early incubation period. To test this, inoculations were made as before and also at intervals of 2, 24, and 72 hours, during which the cut tubers were held in the various humidity conditions to which they were returned after inoculation. One further condition providing 70 per cent humidity with four air changes an hour was established. The intervals selected were presumed, respectively, to suffice (1) for drying the cut surface, (2) for the beginning of cicatrization, and (3) for the apparent healing of the cut by the formation of a new cork layer. To all external appearances these developments actually occurred, but the formation of a wound periderm beneath the cut surface was not at that time followed histologically. The results were as shown in Table 7 and in Plate 1.

In this table the figures for the storage interval December 14 to February 9 (columns 2 and 3) show (1) the general agreement in depth of penetration between two 5-tuber samples which were duplicates except for a difference in position in the chamber during incubation; (2) that the difference in position did not affect the amount of rot. With respect to the data several generalizations can be made: (1) The tendency, observable in Table 6, for *Fusarium trichothecioides* to cause deeper rotting of Green Mountain and Spaulding Rose tubers at the lower humidities is now well marked, particularly in Spaulding Rose. (2) No such regularity is discernible in *F. coeruleum* infections. (3) At 90 per cent humidity or higher there is a slight tendency in all varieties for infection by *F. trichothecioides* to be limited when inoculation occurs 72 hours after cutting. (4) Except for reservations

1 and 3, there is no influence either of humidity or of delayed inoculation on tuber infection by these two species under the conditions here maintained.

TABLE 7.—*Relation of a period of drying under various conditions following cutting to infection of four varieties of potatoes by Fusarium trichothecioides and F. coeruleum*

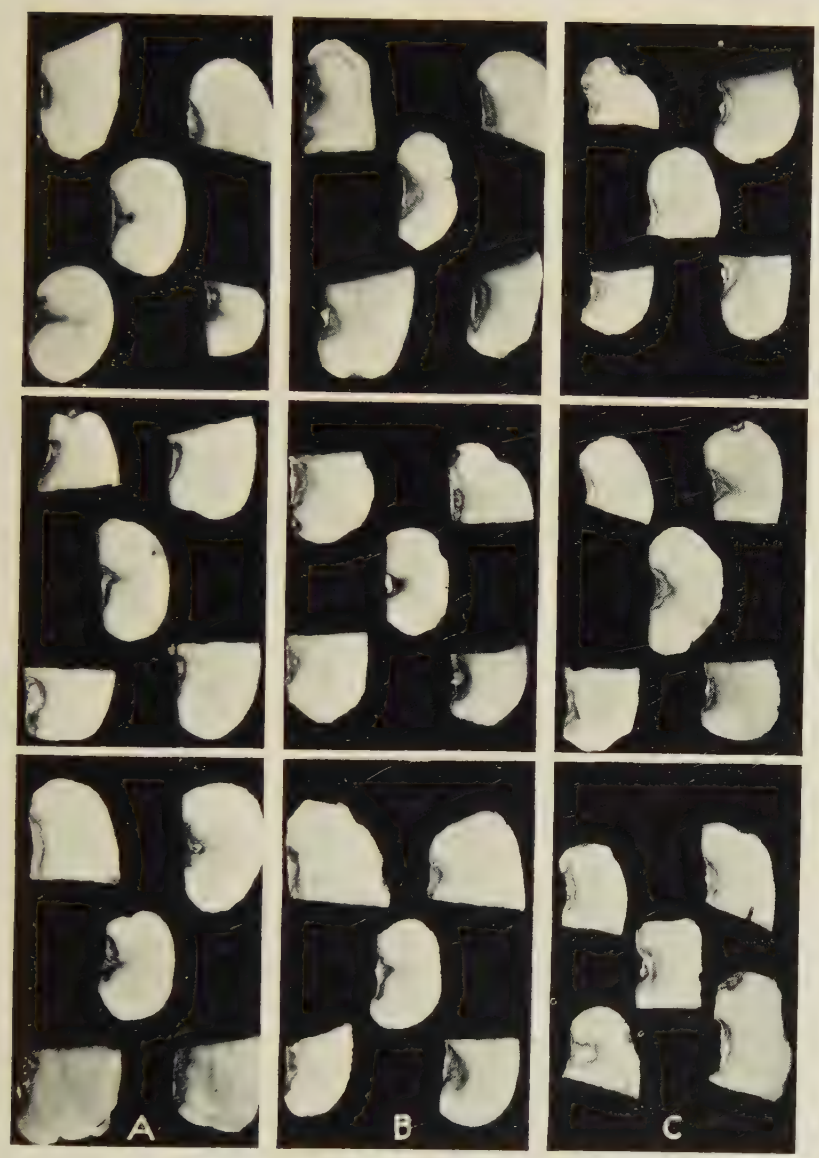
[Data in millimeters, showing the total penetration of five tubers; temperature 6.7° C. In columns 2, 5, 8, and 11 are recorded data in contrast with those of columns 3, 6, 9, and 12, respectively, the two 5-tuber samples in each case being duplicates except for a difference in position in the chamber during incubation]

| Fungus, humidity (per cent), and interval | Potato varieties and period of incubation | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Green Mountain | | | Spaulding Rose | | | Russet Rural | | | White Rural | | |
| | Dec. 14 to Feb. 9 | | Feb. 11 to Mar. 29 | Dec. 14 to Feb. 9 | | Feb. 11 to Mar. 29 | Dec. 14 to Feb. 9 | | Feb. 11 to Mar. 29 | Dec. 14 to Feb. 9 | | Feb. 11 to Mar. 29 |
| 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 |
| F. trichothecioides: | | | | | | | | | | | | |
| 98— At once | 12.0 | 11.0 | 11.0 | 10.0 | 11 | 9.0 | 17 | 16 | 15.0 | 12.0 | 11.0 | 10.0 |
| 2 hours | 15.0 | 12.0 | 8.0 | 12.0 | 12 | 6.5 | 17 | 17 | 15.0 | 12.0 | 14.0 | 7.0 |
| 24 hours | 12.0 | 12.0 | 10.0 | 12.0 | 7 | 5.0 | 14 | 12 | 13.0 | 13.0 | 10.0 | 10.0 |
| 72 hours | 9.0 | 10.0 | 7.0 | 7.0 | 6 | 3.5 | 12 | 8 | 7.0 | 8.5 | 9.0 | 7.0 |
| 90— At once | 19.0 | 12.0 | 11.0 | 16.0 | 8 | 8.0 | 17 | 12 | 12.0 | 12.0 | 14.0 | 15.0 |
| 2 hours | 12.0 | 11.0 | 11.0 | 14.0 | 13 | 11.0 | 20 | 14 | 15.0 | 18.0 | 17.0 | 13.0 |
| 24 hours | 17.0 | 16.0 | 7.0 | 10.0 | 11 | 11.0 | 19 | 13 | 12.0 | 16.0 | 18.0 | 10.0 |
| 72 hours | 11.0 | 8.0 | 3.0 | 10.5 | 10 | 6.0 | 11 | 9 | 4.0 | 4.5 | 3.5 | 4.5 |
| 80— At once | 14.0 | 13.0 | 10.0 | 39.0 | 24 | 6.5 | 15 | 13 | 11.0 | 11.0 | 13.0 | 12.0 |
| 2 hours | 15.0 | 11.0 | 13.0 | 25.0 | 18 | 16.0 | 15 | 13 | 11.0 | 15.0 | 15.0 | 11.0 |
| 24 hours | 13.0 | 14.0 | 10.0 | 14.0 | 22 | 10.0 | 18 | 13 | 12.0 | 13.0 | 12.0 | 15.0 |
| 72 hours | 12.0 | 10.0 | 7.0 | 41.0 | 41 | 14.0 | 14 | 6 | 6.5 | 6.5 | 8.0 | 5.0 |
| 70— At once | 29.0 | 25.0 | 20.0 | 48.0 | 60 | 21.0 | 24 | 19 | 8.0 | 17.0 | 20.0 | 17.0 |
| 2 hours | 35.0 | 36.0 | 24.0 | 39.0 | 40 | 21.0 | 16 | 14 | 14.0 | 14.0 | 27.0 | 18.0 |
| 24 hours | 18.0 | 38.0 | 22.0 | 30.0 | 18 | 34.0 | 29 | 16 | 13.0 | 17.0 | 15.0 | 21.0 |
| 72 hours | 20.0 | 18.0 | 14.0 | 32.0 | 35 | 18.0 | 22 | 15 | 11.0 | 17.0 | 20.0 | 12.0 |
| 70 (with 4 air changes)— At once | 25.0 | 25.0 | 24.0 | 54.0 | 34 | 16.0 | 18 | 12 | 17.0 | 18.0 | 15.0 | 14.0 |
| 2 hours | 15.0 | 27.0 | 17.0 | 53.0 | 25 | 22.0 | 17 | 15 | 16.0 | 16.0 | 15.0 | 13.0 |
| 24 hours | 20.0 | 18.0 | 21.0 | 22.0 | 44 | 23.0 | 17 | 16 | 16.0 | 14.0 | 15.0 | 14.0 |
| 72 hours | 18.0 | 20.0 | 8.5 | 39.0 | 44 | 21.0 | 20 | 13 | 18.0 | 13.0 | 10.0 | 21.0 |
| F. coeruleum: | | | | | | | | | | | | |
| 98— At once | 47.0 | 45.0 | 44.0 | 39.0 | 41 | 30.0 | 35 | 49 | 29.0 | 44.0 | 37.0 | 27.0 |
| 2 hours | 41.0 | 42.0 | 36.0 | 42.0 | 37 | 32.0 | 37 | 33 | 27.0 | 33.0 | 36.0 | 31.0 |
| 24 hours | 48.0 | 43.0 | 38.0 | 33.0 | 33 | 32.0 | 36 | 33 | 36.0 | 30.0 | 28.0 | 36.0 |
| 72 hours | 41.0 | 38.0 | 37.0 | 34.0 | 32 | 29.0 | 42 | 48 | 29.0 | 37.0 | 33.0 | 33.0 |
| 90— At once | 39.0 | 38.0 | 34.0 | 38.0 | 40 | 26.0 | 43 | 50 | 29.0 | 48.0 | 43.0 | 37.0 |
| 2 hours | 42.0 | 50.0 | 32.0 | 49.0 | 46 | 31.0 | 56 | 25 | 28.0 | 36.0 | 32.0 | 32.0 |
| 24 hours | 39.0 | 36.0 | 29.0 | 44.0 | 43 | 23.0 | 36 | 36 | 23.0 | 35.0 | 40.0 | 28.0 |
| 72 hours | 35.0 | 41.0 | 31.0 | 40.0 | 56 | 29.0 | 36 | 40 | 41.0 | 42.0 | 46.0 | 41.0 |
| 80— At once | 36.0 | 34.0 | 33.0 | 27.0 | 31 | 21.0 | 37 | 40 | 29.0 | 40.0 | 35.0 | 35.0 |
| 2 hours | 32.0 | 36.0 | 18.0 | 27.0 | 28 | 17.0 | 41 | 35 | 22.0 | 40.0 | 32.0 | 20.0 |
| 24 hours | 39.0 | 45.0 | 12.0 | 35.0 | 35 | 26.0 | 35 | 34 | 27.0 | 28.0 | 34.0 | 25.0 |
| 72 hours | 26.0 | 39.0 | 30.0 | 28.0 | 38 | 25.0 | 39 | 33 | 24.0 | 45.0 | 45.0 | 18.0 |
| 70— At once | 36.0 | 41.0 | 9.0 | 64.0 | 44 | 22.0 | 25 | 42 | 12.0 | 41.0 | 37.0 | 17.0 |
| 2 hours | 38.0 | 39.0 | 12.0 | 39.0 | 36 | 19.0 | 38 | 42 | 9.0 | 37.0 | 26.0 | 15.0 |
| 24 hours | 41.0 | 22.0 | 13.0 | 17.0 | 19 | 22.0 | 44 | 33 | 11.0 | 46.0 | 44.0 | 20.0 |
| 72 hours | 16.5 | 21.5 | 13.0 | 17.0 | 17 | 24.0 | 30 | 29 | 19.0 | 28.0 | 30.0 | 8.0 |
| 70 (with 4 air changes)— At once | 51.0 | 50.0 | 20.0 | 32.0 | 27 | 22.0 | 42 | 35 | 26.0 | 32.0 | 50.0 | 24.0 |
| 2 hours | 34.0 | 39.0 | 16.5 | 51.0 | 33 | 21.0 | 48 | 35 | 22.0 | 44.0 | 37.0 | 23.0 |
| 24 hours | 36.0 | 52.0 | 25.0 | 37.0 | 31 | 25.0 | 51 | 41 | 27.0 | 39.0 | 45.0 | 25.0 |
| 72 hours | 21.0 | 35.0 | 27.0 | 28.0 | 38 | 21.0 | 51 | 41 | 30.0 | 28.0 | 26.0 | 19.0 |

One can reasonably object that inoculations made with a mass of mycelium on an agar medium do not simulate natural infection. It is usually assumed that inoculation with a spore suspension more faithfully reflects conditions obtaining in the field. Possibly in respect to *Fusarium trichothecioides* this is true, as this species sporulates freely upon almost any medium, whereas chlamydospores are rare. On the other hand, *F. coeruleum* usually sporulates but scantily on artificial media, and often not abundantly upon decaying potatoes, but chlamydospores are typically produced. Mycelium inoculations in this case would typify natural infection more nearly than spore suspensions, but the use of the agar medium may still be condemned. Results from inoculations with soil cultures, thus faithfully copying field conditions, will be given later. Although the writers have made use of spore suspensions for inoculation in this work, it is with the conviction that this practically defeats the aim of controlling humidity, as the addition of the spore-carrying liquid probably determines the conditions under which germination and entry take place, irrespective of the humidity. In the dissipation of the water film probably the rate of air exchange and not the relative saturation is the determining factor. At any rate, it is the factor that is most susceptible of control in practical storage, and if the data here given demonstrate that wounds may be susceptible to infection for a considerable time if they remain wet, it points to the greater importance of drying the stock before storage begins than of regulating the humidity thereafter.

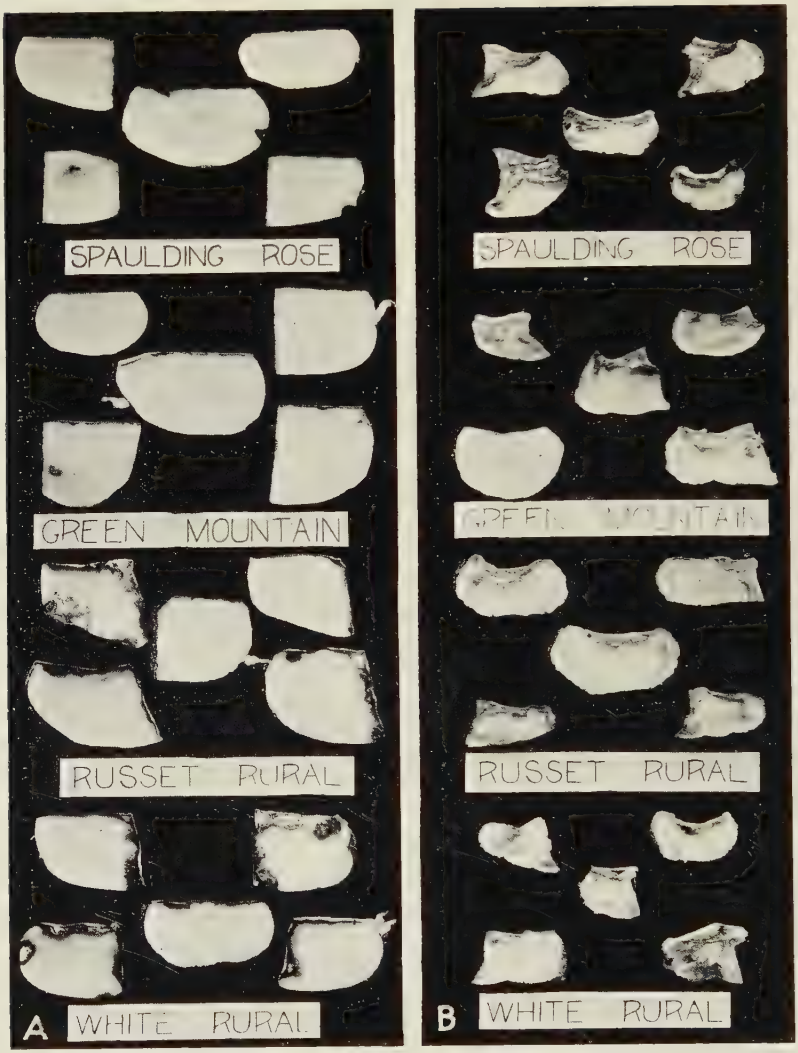
The results from spore-suspension inoculations are given in Table 8 and shown in Plates 2 and 3. The same storage chambers were used as before at a temperature of 6.7° C., but one additional condition was provided in the main storage cellar, where the temperature averaged about 10°, the relative humidity 80 per cent, and copious natural ventilation occurred through openings at each end. In one experiment an examination was made six weeks after inoculation, but the tubers were not cut and measured until five weeks later. As the rot advanced considerably during the second interval, it is evident that such slight infections as are reported after five weeks had not necessarily attained their maximum development, though in many cases they were found to be apparently blocked out by the wound-healing response of the tuber.

No infection by *Fusarium trichothecioides* occurred in either experiment at the relative humidities of 90 or 98 per cent. On the other hand, 100 per cent infection occurred several times at 70 per cent humidity, and no difference appeared to result from nearly stationary as against circulating air. This supports the suggestion previously made that in spore-suspension inoculations the addition of a water film counteracts any direct effect of humidity on the infection process. *F. coeruleum*, on the other hand, shows consistently a higher percentage of infection at the high humidities. The total depth of penetration per tuber is not, however, greater at the high humidities; in several instances the reverse is true. As it is scarcely conceivable that germination—a process requiring absorption of water—is favored by low humidity or rapid evaporation, these circumstances may best be explained by assuming that at the temperature employed some process other than germination and probably independent of




EFFECT OF HUMIDITY AND AN INTERVAL FOLLOWING INOCULATION ON INFECTION OF RUSSET RURAL POTATOES BY MYCELIUM OF FUSARIUM COERULEUM

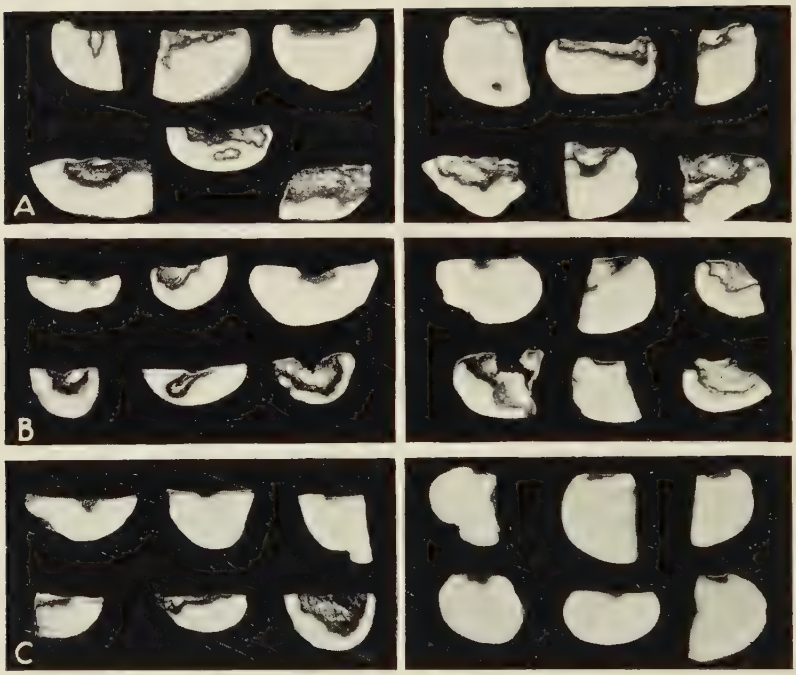
A, 95 per cent humidity; B, 90 per cent humidity; C, 70 per cent humidity. In each lettered figure the bottom group of five tubers was inoculated at once after cutting, the middle group after an interval of 24 hours, the top group 72 hours.




EFFECT OF HUMIDITY ON INFECTION OF DIFFERENT VARIETIES OF POTATOES BY GERMINATING SPORES OF FUSARIUM COERULEUM

Left column 95 per cent humidity, right column 70 per cent humidity, temperature 6.7° C.

INFECTION OF FOUR VARIETIES OF POTATOES BY GERMINATING SPORES OF FUSARIUM TRICHOTHECIOIDES AFTER INCUBATION AT 6.7° C. AND 70 PER CENT HUMIDITY




INFECTION OF SIX VARIETIES OF POTATOES INOCULATED WITH MYCELIUM OF FUSARIUM SULPHUREUM 10 DAYS AFTER CUTTING

A, incubated at 2° C.; B, incubated at 5° C.; C, incubated at 7.5° C. In each lettered figure, the group of six tubers at the left shows infection of median sections, the group at the right infection of tangential sections. In each group the varieties reading left to right are: Top—Irish Cobbler, Spaulding Rose, Triumph; bottom—White Rural, Green Mountain, Russet Rural

TABLE 8.—*Relation of a period of drying under various conditions following cutting to infection of four varieties of potatoes by spore suspensions of Fusarium trichothecioides and F. coeruleum*

[Data given in millimeters show the total penetration of five tubers]

| Fungus, humidity (per cent), and time interval | Potato varieties and period of drying | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Green Mountain | | | | Spaulding Rose | | | | Russet Rural | | | | White Rural | | | |
| | Mar. 31 to May 6 | | Feb. 12 to May 6 | | Mar. 31 to May 6 | | Feb. 12 to May 6 | | Mar. 31 to May 6 | | Feb. 12 to May 6 | | Mar. 31 to May 6 | | Feb. 12 to May 6 | |
| | *P. ct.* | *Mm.* | *P. ct.* | *Mm.* | *P. ct.* | *Mm.* | *P. ct.* | *Mm.* | *P. ct.* | *Mm.* | *P. ct.* | *Mm.* | *P. ct.* | *Mm.* | *P. ct.* | *Mm.* |
| F. trichothecioides: | | | | | | | | | | | | | | | | |
| 98, At once | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 98, 2 hours | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 98, 8 hours | 0 | 0 | | | 0 | 0 | | | 0 | 0 | | | 0 | 0 | | |
| 98, 24 hours | 0 | 0 | | | 0 | 0 | | | 0 | 0 | | | 0 | 0 | | |
| 90, At once | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 90, 2 hours | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 90, 8 hours | 0 | 0 | | | 0 | 0 | | | 0 | 0 | | | 0 | 0 | | |
| 90, 24 hours | 0 | 0 | | | 0 | 0 | | | 0 | 0 | | | 0 | 0 | | |
| 80, At once | 80 | 5.0 | 0 | 0 | 0 | 0 | 100 | 27.0 | 80 | 5.5 | 20 | 10.0 | 40 | 1.0 | 60 | 9.5 |
| 80, 2 hours | 60 | 1.5 | 0 | 0 | 40 | 1.0 | 60 | 11.5 | 40 | 1.0 | 0 | 0 | 40 | 1.0 | 0 | 0 |
| 80, 8 hours | 80 | 2.5 | | | 80 | 4.5 | | | 80 | 2.0 | | | 60 | 1.5 | | |
| 80, 24 hours | 40 | 4.0 | | | 60 | 4.5 | | | 40 | 1.0 | | | 60 | 1.5 | | |
| 70, At once | 60 | 7.5 | 100 | 29.0 | 0 | 0 | 100 | 47.0 | 40 | 2.0 | 100 | 34.5 | 100 | 2.5 | 80 | 16.0 |
| 70, 2 hours | 80 | 9.5 | 80 | 26.0 | 40 | 1.0 | 80 | 30.0 | 80 | 3.0 | 100 | 26.0 | 100 | 4.0 | 60 | 21.0 |
| 70, 8 hours | 100 | 11.0 | | | 80 | 6.0 | | | 80 | 3.0 | | | 100 | 6.0 | | |
| 70, 24 hours | 100 | 7.5 | | | 40 | 1.0 | | | 20 | 1.0 | | | 20 | 1.0 | | |
| 70 (with 4 air changes), At once | 80 | 4.5 | 100 | 35 | 20 | .5 | 60 | 45.0 | 100 | 6.0 | 80 | 10.5 | 100 | 10.0 | 20 | 3.0 |
| 70 (with 4 air changes), 2 hours | 60 | 4.0 | 0 | 0 | 20 | .5 | 0 | 0 | 80 | 6.0 | 80 | 19.0 | 100 | 2.5 | 0 | 0 |
| 70 (with 4 air changes), 8 hours | 100 | 11.0 | | | 40 | 1.0 | | | 100 | 3.5 | | | 100 | 4.0 | | |
| 70 (with 4 air changes), 24 hours | 80 | 4.0 | | | 0 | 0 | | | 40 | 1.0 | | | 0 | 0 | | |
| Cellar, At once | 100 | 4.0 | | | 40 | 1.0 | | | 60 | 1.5 | | | 100 | 2.5 | | |
| Cellar, 2 hours | 100 | 2.5 | | | 40 | 1.0 | | | 80 | 2.0 | | | 60 | 2.0 | | |
| Cellar, 8 hours | 40 | 1.0 | | | 40 | 1.0 | | | 80 | 2.0 | | | 60 | 1.5 | | |
| Cellar, 24 hours | 80 | 4.5 | | | 40 | 1.5 | | | 100 | 3.0 | | | 100 | 4.0 | | |
| F. coeruleum: | | | | | | | | | | | | | | | | |
| 98, At once | 100 | 2.5 | 80 | 7.5 | 60 | 1.5 | 20 | 3.0 | 80 | 5.0 | 100 | 28.0 | 100 | 8.5 | 80 | 19.5 |
| 98, 2 hours | 100 | 3.0 | | | 100 | 2.5 | | | 100 | 6.0 | | | 100 | 6.0 | | |
| 98, 8 hours | 100 | 4.5 | | | 100 | 7.5 | | | 100 | 11.0 | | | 100 | 10.0 | | |
| 98, 24 hours | 100 | 6.5 | | | 100 | 7.0 | | | 100 | 11.0 | | | 100 | 11.0 | | |

TABLE 8.—*Relation of a period of drying under various conditions following cutting to infection of four varieties of potatoes by spore suspensions of Fusarium trichothecioides and F. coeruleum*—Continued

[Data given in millimeters show the total penetration of five tubers]

| Fungus, humidity (per cent), and time interval | Potato varieties and period of drying | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Green Mountain | | | | Spaulding Rose | | | | Russet Rural | | | | White Rural | | | |
| | Mar. 31 to May 6 | | Feb. 12 to May 6 | | Mar. 31 to May 6 | | Feb. 12 to May 6 | | Mar. 31 to May 6 | | Feb. 12 to May 6 | | Mar. 31 to May 6 | | Feb. 12 to May 6 | |
| F. Coeruleum: | *P. ct.* | *Mm.* | *P. ct.* | *Mm.* | *P. ct.* | *Mm.* | *P. ct.* | *Mm.* | *P. ct.* | *Mm.* | *P. ct.* | *Mm.* | *P. ct.* | *Mm.* | *P. ct.* | *Mm.* |
| 90, At once | 40 | 1.0 | 100 | 15.5 | 60 | 1.5 | 80 | 5.5 | 100 | 8.0 | 80 | 24.0 | 80 | 2.5 | 100 | 45.0 |
| 90, 2 hours | 20 | .5 | | | 40 | 1.5 | | | 100 | 7.0 | | | 100 | 13.0 | | |
| 90, 8 hours | 80 | 2.5 | | | 60 | 8.0 | | | 100 | 9.0 | | | 80 | 3.5 | | |
| 90, 24 hours | 80 | 6.0 | | | 100 | 5.0 | | | 100 | 8.0 | | | 100 | 10.0 | | |
| 80, At once | 100 | 6.0 | 100 | 5.5 | 100 | 5.0 | 100 | 26.0 | 100 | 4.0 | 100 | 20.0 | 100 | 7.0 | 100 | 47.0 |
| 80, 2 hours | 40 | 1.0 | | | 100 | 2.5 | | | 100 | 4.5 | | | 100 | 5.0 | | |
| 80, 8 hours | 60 | 3.0 | | | 100 | 2.5 | | | 100 | 3.5 | | | 100 | 8.0 | | |
| 80, 24 hours | 100 | 4.0 | | | 60 | 3.0 | | | 100 | 3.0 | | | 100 | 12.0 | | |
| 70, At once | 40 | 1.5 | 100 | 37.0 | 0 | 0 | 100 | 33.0 | 100 | 4.5 | 100 | 32.0 | 100 | 3.0 | 100 | 30.0 |
| 70, 2 hours | 80 | 2.0 | | | 0 | 0 | | | 80 | 2.0 | | | 100 | 4.5 | | |
| 70, 8 hours | 40 | 1.0 | | | 20 | .5 | | | 40 | 1.0 | | | 100 | 4.0 | | |
| 70, 24 hours | 60 | 1.5 | | | 0 | 0 | | | 100 | 2.5 | | | 60 | 2.5 | | |
| 70 (with 4 air changes), At once | 60 | 3.5 | 60 | 26.5 | 20 | .5 | 40 | 1.0 | 100 | 4.0 | 60 | 23.0 | 60 | 2.5 | 100 | 27.5 |
| 70 (with 4 air changes), 2 hours | 60 | 1.5 | | | 20 | 1.0 | | | 40 | 1.0 | | | 100 | 2.5 | | |
| 70 (with 4 air changes), 8 hours | 60 | 2.0 | | | 20 | .5 | | | 40 | 1.0 | | | 100 | 3.5 | | |
| 70 (with 4 air changes), 24 hours | 80 | 4.0 | | | 40 | 2.0 | | | 80 | 5.5 | | | 20 | .5 | | |
| Cellar, At once | 100 | 4.5 | | | 40 | 1.0 | | | 20 | .5 | | | 60 | 1.5 | | |
| Cellar, 2 hours | 100 | 2.5 | | | 100 | 2.5 | | | 100 | 3.0 | | | 40 | 1.0 | | |
| Cellar, 8 hours | 40 | 1.0 | | | 80 | 2.0 | | | 0 | 0 | | | 20 | .5 | | |
| Cellar, 24 hours | 60 | 1.5 | | | 80 | 2.0 | | | 40 | 1.0 | | | 60 | 1.5 | | |

the growth of the parasite actually determines whether infection occurs. The wound-healing process in the potato tuber suggests itself as very likely to be the determining factor.

Before investigating the relation of infection to wound-periderm formation, several attempts were made to determine whether humidities lower than heretofore employed might influence infection. A storage chamber similar to the others was maintained at 6.7° C., and the humidity was regulated manually at 50 per cent, with a variance of 5 per cent each way. To furnish for comparison degrees of humidity somewhat above 50 per cent, four desiccators were connected in series and air passed through at a measured rate. The humidity in each was estimated by determining the weight loss of uninoculated tubers kept in the same desiccators, this being regarded as water loss. Evidently there would be decreasing amounts of evaporation as the distance increased from the inlet where air at 50 per cent humidity entered. If this water loss was proportional to the evaporating power of the air, it appears from the data that the saturation deficit in the terminal desiccator was only one-fourth to one-fifth that of the inlet desiccator, yet five tubers inoculated with *Fusarium coeruleum* in each desiccator showed within 1 mm. the same total decay. No difference resulted from varying the rate of air exchange from one to four times an hour except that the evaporation throughout the series of desiccators tended to become equalized as the rate increased. When the inoculated tubers were subjected to such rapid evaporation as resulted from exposure to the large volume of half-saturated air in the room, marked shriveling resulted, yet infection of the four varieties by *F. coeruleum* and *F. trichothecioides* occurred, with penetration averaging 1 to 4 mm. per tuber. The limited amount of decay is due to low temperature and the short interval and to marked shriveling of the cut tubers.

#### RELATION OF INFECTION TO KIND OF INJURY AND ITS HEALING

Moore (*15*) made note of the infection by *Fusarium coeruleum* of a 7-day-old wound but gave no details as to its occurence. Löhnis (*13*) stated that tubers which had lain in the field for six days were still susceptible to infection by *Phytophthora infestans* through the wounds incurred during digging. Various workers studying suberization and wound-periderm formation in potato tubers have referred to the effect of warmth and a moist atmosphere on the process. Priestley (*24*) and others have observed that potato varieties differ in the readiness with which wounds are healed. No data have been found indicating what time is required under known conditions of temperature and humidity for healing to attain morphological completion, or, what is perhaps more important, the stage at which protection against various disease organisms is secure.

A preliminary experiment to determine how long tubers remain susceptible to infection through harvesting injuries was carried out in September, 1925. Tubers of four varieties were subjected to artificial injuries simulating the three forms that occur in the field—skinning, cutting, and bruising—then, after various intervals in

different storage conditions, were inoculated with several typical rot organisms.

To skin the tubers they were scraped with a knife so as to separate the periderm at the cambium without much injury to the underlying tissues. Cutting was done with a blunt hatchet so as to leave a gaping wound. Bruising was done with the knurled head of the hatchet, which both crushed the tissue and broke the skin. The work was carried out with reasonably aseptic precautions, and no difficulty was experienced on account of contaminating organisms except at 21° C., where a few cases of bacterial rot occurred. In two of the subsequent storage conditions the air was practically saturated and the temperature respectively 6.7° and 21° C. (44° and 70° F.). In the other—representing good cellar storage with abundant ventilation—the temperature averaged 11° C. (52° F.) and the humidity 80 per cent. For inoculation, agar cultures of *Fusarium coeruleum* and *Phytophthora infestans* and a broth culture of *Bacillus carotovorus* were used. The broth culture failed to infect in all trials. Following inoculation all lots were placed at 10° C. and 80 per cent humidity, where they remained one month. The results with *F. coeruleum* are shown in Table 9 and with *P. infestans* in Table 10.

TABLE 9.—*Relation of kind of injury and temperature and humidity of holding conditions to infection of two varieties of potatoes by Fusarium coeruleum, showing percentage of infection and total penetration (millimeters) of five tubers*

| Storage temperature, humidity (per cent), and inoculation interval | Spaulding Rose | | | | | | Russet Rural | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Skinned | | Cut | | Bruised | | Skinned | | Cut | | Bruised | |
| | *Pct.* | *Mm.* | *Pct.* | *Mm.* | *Pct.* | *Mm.* | *Pct.* | *Mm.* | *Pct.* | *Mm.* | *Pct.* | *Mm.* |
| 6.7° C., 98 — At once | | | | | | | | | | | | |
| 6.7° C., 98 — 1 day | 100 | 13 | 100 | 11 | 40 | 2 | 100 | 6 | 100 | 34 | 80 | 12 |
| 6.7° C., 98 — 2 days | 60 | 2 | 100 | 9 | 80 | 6 | 100 | 9 | 100 | 23 | 80 | 10 |
| 6.7° C., 98 — 3 days | 100 | 6 | 100 | 6 | 20 | 1 | 60 | 2 | 100 | 21 | 100 | 8 |
| 11° C., 80 (cellar) — At once | 80 | 7 | 80 | 12 | 80 | 24 | 80 | 9 | 100 | 35 | 100 | 27 |
| 11° C., 80 (cellar) — 1 day | 100 | 14 | 100 | 29 | 80 | 5 | 60 | 2 | 100 | 24 | 100 | 25 |
| 11° C., 80 (cellar) — 2 days | 80 | 5 | 100 | 15 | 100 | 4 | 40 | 3 | 100 | 26 | 100 | 8 |
| 11° C., 80 (cellar) — 3 days | 100 | 6 | 100 | 5 | 40 | 1 | 80 | 3 | 100 | 27 | 100 | 18 |
| 21° C., 98 — At once | | | | | | | | | | | | |
| 21° C., 98 — 1 day | 60 | 3 | 60 | 5 | 100 | 8 | 40 | 7 | 100 | 13 | 100 | 13 |
| 21° C., 98 — 2 days | 0 | 0 | 20 | 1 | 40 | 1 | 0 | 0 | 100 | 19 | 100 | 52 |
| 21° C., 98 — 3 days | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 80 | 14 | 100 | 16 |

Worthy of note is the failure of holding at low temperature, whether in a very humid or a dry well-ventilated atmosphere, to render wounds immune to Fusarium infection; whereas in two varieties, Green Mountain and Spaulding Rose, healing was nearly complete after two days at 21°. That the White Rural and Russet Rural varieties are slower to heal is evident in all cuts and bruises becoming infected even after three days at this temperature. A mild injury from skinning becomes resistant to Fusarium infection more rapidly than cuts or bruises, but remains susceptible to Phytophthora; whereas bruises and cuts in which tissue necrosis is greater were not even initially very susceptible to this fungus. This is due, it would seem, to its well-known avoidance of a saprophytic habit on potato tissue.

TABLE 10.—*Relation of kind of injury and temperature and humidity of holding conditions to infection of two varieties of potatoes by Phytophthora infestans, showing infection (+) and absence of infection (0) in two tubers*

| Storage conditions | Green Mountain | | | | | | | | | White Rural | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Inoculated | Uninjured | | Skinned | | Cut | | Bruised | | Inoculated | Uninjured | | Skinned | | Cut | | Bruised | |
| | | Tubers | Result | Tubers | Result | Tubers | Result | Tubers | Result | | Tubers | Result | Tubers | Result | Tubers | Result | Tubers | Result |
| Cellar | At once | 2 | 0 | 2 | + | 2 | ---- | 1 | 0 | At once | 2 | 0 | 2 | + | 2 | + | 2 | 0 |
| | | | | | | | | 1 | + | | | | | | | | | |
| | After 3 days. | 2 | 0 | 2 | + | 1 | 0 | 1 | 0 | After 100 hours. | 2 | 0 | 2 | 0 | 2 | + | 2 | 0 |
| | | | | | | 1 | + | 1 | + | | | | | | | | | |
| 21° C | do | 2 | 0 | 2 | 0 | 2 | 0 | 2 | 0 | do | 2 | 0 | 2 | 0 | 2 | 0 | 2 | 0 |
| 6.7° C | do | 2 | 0 | 2 | + | 2 | 0 | 2 | 0 | do | 2 | + | 2 | + | 2 | + | 2 | 0 |

Subsequent experiments gave further evidence that exposure of cut tubers for 24 or 48 hours in a saturated atmosphere at 21° to 24° C. is insufficient to protect Green Mountain or Rural tubers against mycelium inoculations with *Fusarium coeruleum*, but that infection is practically suppressed when the interval is three days and the temperature is 25° or above. Appel (*1*) found that the suberization layer which forms over a cut surface within 24 hours when it is exposed to a moist atmosphere, protects the tuber against infection by *Bacillus phytophthorus*. It is evident, however, that this protection is inadequate against *F. coeruleum*. Not until the wound periderm which, according to Appel, is not initiated until the lapse of 48 to 60 hours, is at least well begun, is complete protection afforded. The manner of penetration through the suberization layer was not determined, though it may be noted that the entry of fungi through suberin lamellae, so far as it has been observed, is always by mechanical pressure unaided by enzyme action. The wound periderm, however, when fully formed, excludes all species of Fusarium yet tested as effectively as the normal periderm.

In their work on suberization in potato tubers, Priestley and Woffenden (*24*) stated that a quantitative expression for the suberization process had not been found, since its detection depended on a nonquantitative microchemical test; but they recognized the influence of temperature on this and on phellogen activity, showing that in some varieties the rate of phelloderm regeneration at 25° is twice that at 15° C. and that the process may be delayed as long as 12 days at the lower temperature. It appeared to the writers that a study of the infection of cut tubers by the wound-parasitic Fusaria would afford an index of the effect of temperature and other factors on this process in different potato varieties.

As a prerequisite to such a test, the effects of several possible factors required attention. The evidence in the literature is consistently in support of the greater susceptibility to wound rots of tubers that have sprouted or have been long in storage, a condition believed by Shapovalov and Edson (*25*) to be due to reduced water content, though, according to Kny (*9*), immature tubers react more quickly than

mature ones to wound stimulation. The results already presented, however, do not point to any great importance of the age factor if the tubers have reached maturity in the field and are stored under conditions that prevent sprouting and undue desiccation. The position of the wound with respect to the vascular tissue is believed to influence the rate of healing, since it is held that the substance which stimulates the wound meristem to form diffuses from the phloem. In the potato tuber the phloem is so intricately distributed that no considerable area, except the central pith, is untraversed by it. Whether the healing of deep wounds would differ from that of shallow remained for experiments to show.

A preliminary test, carried out with the Irish Cobbler variety inoculated after different periods of holding at temperatures ranging from

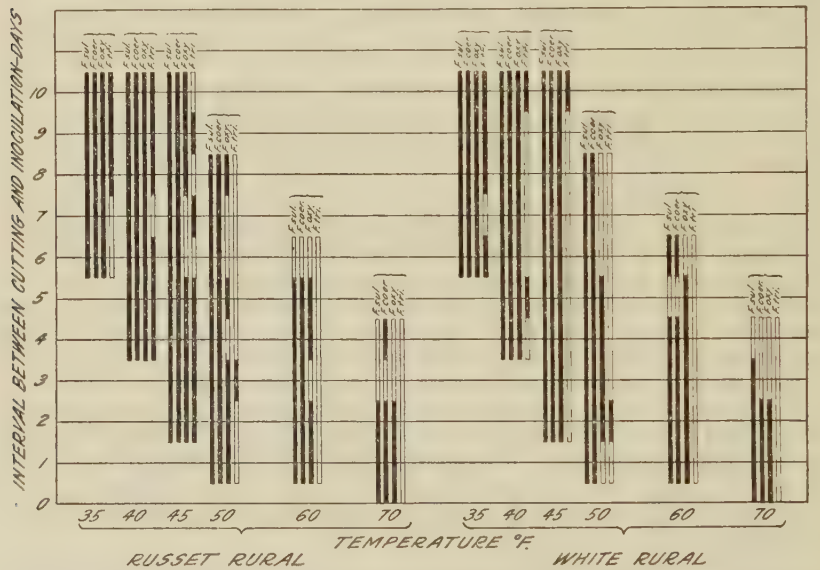



FIG. 2.—Diagram showing the relation of time and temperature to wound healing and infection of the Russet Rural and White Rural varieties of potato by *Fusarium sulphureum*, *F. coeruleum*, *F. trozysporum*, and *F. trichothecioides*

0° to 35° C., showed that healing was complete so far as infection by *Fusarium oxysporum* was concerned, after 1 day at 35° or 2 days at 30°, but was not after 10 days at 0° or 5°.

### EFFECT OF SUBERIZATION AND WOUND-PERIDERM FORMATION ON INFECTION

Comprehensive experiments were then carried out to test simultaneously the effect of temperature on the suberization and healing of cut surfaces in different varieties of potatoes and of the ability of four species of Fusarium to infect through partly healed wounds. Six varieties, namely, Russet Rural, White Rural, Green Mountain, Spaulding Rose, Irish Cobbler, and Triumph, were included. Five tubers constituted a test lot. One lot of each variety was cut by removing a tangential slice 5 to 10 mm. thick so as to pass through or outside the vascular ring, and one was cut approximately through the middle.

Separate lots were prepared for inoculation by each of the following species: *F. sulphureum*, *F. coeruleum*, *F. trichothecioides*, and *F. oxysporum*. One lot was inoculated immediately, and from five to nine lots were placed at each of the temperatures 1.7°, 4.4°, 7.3°, 10°, 15.5°, and 21.1° C. (35°, 40°, 45°, 50°, 60°, and 70° F.), in accordance with the indications given in the preliminary experiment of the number of days required at each temperature for healing to be complete. At intervals of 24 hours these lots were withdrawn one by one for 10 days and inoculated the same as the first. Following inoculation all lots were placed in a chamber maintained at approximately 15° to 18° C. and 90 per cent humidity. This temperature was somewhat less favorable for the growth of *F. oxysporum* than for the other three species, but

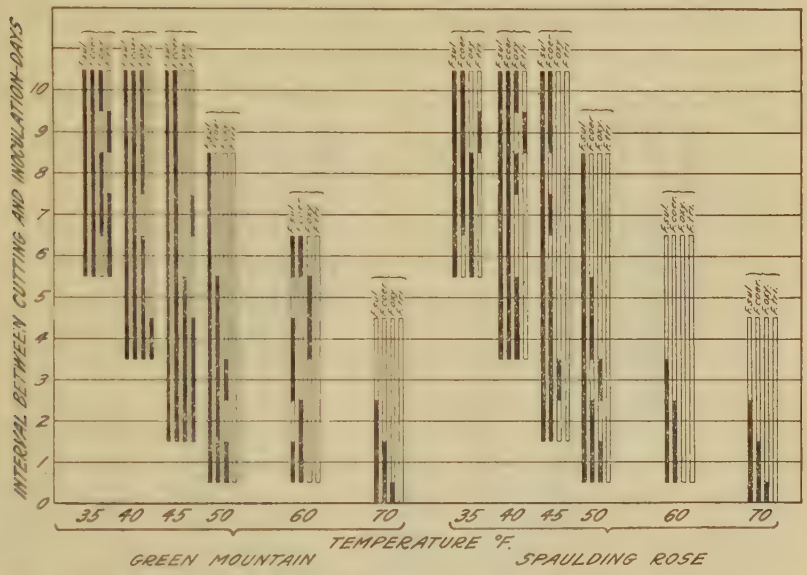



FIG. 3.—Diagram showing the relation of time and temperature to wound healing and infection of the Green Mountain and Spaulding Rose varieties of potato by *Fusarium sulphureum*, *F. coeruleum*, *F. oxysporum*, and *F. trichothecioides*

was well within the range at which all species can cause rot. It was selected in preference to higher temperatures because of the greater ease of maintaining high humidity, thus avoiding marked shrinkage of the cut tubers, which might invalidate measurements of penetration. This suboptimal temperature for *F. oxysporum* should be considered in comparing the amount of rot caused by the different species, as shown in the accompanying diagrams. (Figs. 2, 3, and 4.)

In each lot of five tubers, four were inoculated by placing squares of medium and mycelium from agar cultures in Petri dishes on the cut surface. From the fifth tuber in each lot a sample was taken, at the same time the others were inoculated, and this was fixed in chrom-acetic acid and sectioned in paraffin. These samples, supplemented by others from diverse experiments, formed the basis for the histological study of suberization and wound-periderm for-

mation in the potato reported by Artschwager (1). In all, 480 lots of four tubers were inoculated. They were examined after eight weeks of storage.

A specimen compilation of results is shown in Table 11. From 24 similar tables Figures 2, 3, and 4 were constructed. In the graphic presentation all instances of penetration less than 2 millimeters were rejected as negative, in accordance with the actual finding that such limited advance of decay in two months at a favorable temperature was generally due to blocking by the wound periderm.

In respect to the rate of healing of tangential and median cuts, definite evidence was secured in two varieties, Russet Rural and White Rural, that a protective layer develops more rapidly under the skin-lower injury. In other varieties the trend of evidence in this direction was less marked, and there were occasional reversals of the rule that

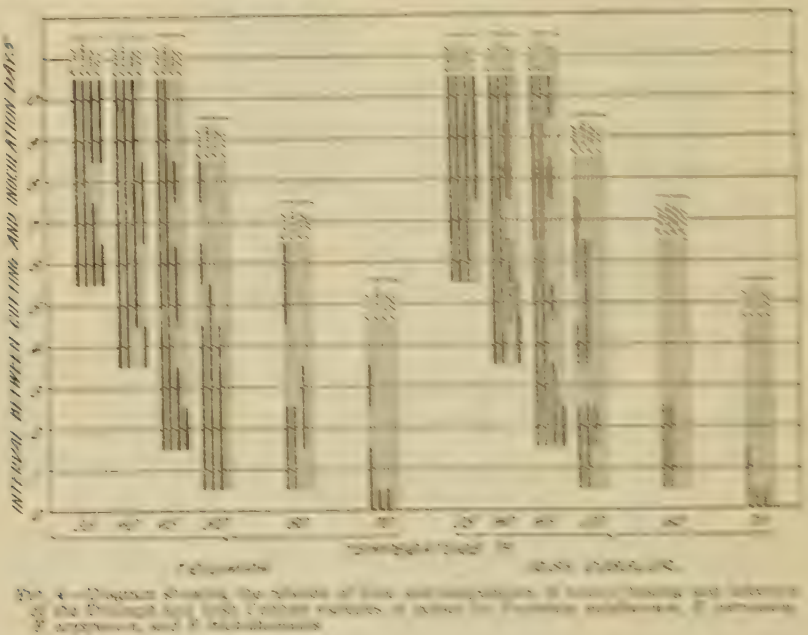


FIG. 4.—Diagram showing the relation of time and temperature to healing (tissue and infection) of [illegible] tuber cuttings. [illegible] parenchyma, and P periderm.

median cuts showed more frequent and deeper infections, but there is sufficient support to indicate that this is a general relation. A difference in the rate of healing is of course to be sought only when the time-temperature factor is favorable to wound-periderm formation. With the temperatures and intervals here employed, the production of a wound periderm was practically limited to a temperature of 15° C. or above. In Table 11 all the data pertaining to 15° and higher temperatures admit of a comparison between the median and tangential positions with respect to periderm formation. These data show that the percentage of infection through median cuts and the depth of penetration are greater in every instance. When the time-temperature factor was very favorable to healing, infection in the tangential position failed entirely, though some progress was still made through median cuts.

TABLE 11.—*Effect of temperature and time on healing of cut tubers as shown by infection by Fusarium spp.*

[Specimen sheet of infection of Russet Rural variety by *Fusarium sulphureum*, showing the percentage of infection and total penetration (millimeters) in four tuber samples]

| Temperature and position of cut | Items | Interval between cutting and inoculation (days) | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | 0 | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 |
| 1.7° C. Median | Per cent | .. | ..... | ..... | ..... | ..... | ..... | 75 | 100 | 100 | 75 | 100 |
| | Millimeters | .. | ..... | ..... | ..... | ..... | ..... | 31 | 36 | 45 | 40 | 86 |
| 1.7° C. Tangential | Per cent | .. | ..... | ..... | ..... | ..... | ..... | 75 | 100 | 100 | 100 | 75 |
| | Millimeters | .. | ..... | ..... | ..... | ..... | ..... | 27 | 78 | 57 | 80 | 60 |
| 4.4° C. Median | Per cent | .. | ..... | ..... | ..... | 75 | 100 | 100 | 50 | 100 | 100 | 100 |
| | Millimeters | .. | ..... | ..... | ..... | 9 | 44 | 31 | 34 | 51 | 39 | 82 |
| 4.4° C. Tangential | Per cent | .. | ..... | ..... | ..... | 100 | 100 | 100 | 100 | 75 | 75 | 100 |
| | Millimeters | .. | ..... | ..... | ..... | 38 | 35 | 22 | 57 | 51 | 45 | 48 |
| 7.3° C. Median | Per cent | .. | ..... | 75 | 50 | 50 | 75 | 50 | 50 | 100 | 100 | 50 |
| | Millimeters | .. | ..... | 43 | 4 | 26 | 28 | 4 | 14 | 35 | 18 | 40 |
| 7.3° C. Tangential | Per cent | .. | ..... | None. | 75 | 50 | 25 | 100 | 75 | 50 | 100 | 100 |
| | Millimeters | .. | ..... | ..... | 8 | 5 | 20 | 9 | 9 | 7 | 41 | 22 |
| 10° C. Median | Per cent | .. | 75 | 100 | 100 | 50 | 100 | 75 | 75 | 50 | --- | --- |
| | Millimeters | .. | 12 | 9 | 37 | 7 | 22 | 14 | 10 | 9 | --- | --- |
| 10° C. Tangential | Per cent | .. | 50 | 50 | 25 | 25 | 25 | None. | None. | None. | --- | --- |
| | Millimeters | .. | 8 | 7 | 4 | 5 | 4 | ..... | ..... | ..... | --- | --- |
| 15.5° C. Median | Per cent | .. | 100 | 75 | 50 | 50 | 50 | ..... | ..... | ..... | --- | --- |
| | Millimeters | .. | 94 | 26 | 7 | 4 | 22 | None. | ..... | ..... | --- | --- |
| 15.5° C. Tangential | Per cent | .. | 50 | None. | None | None. | None. | None. | ..... | ..... | --- | --- |
| | Millimeters | .. | 8 | ..... | ..... | ..... | ..... | ..... | ..... | ..... | --- | --- |
| 21.1° C. Median | Per cent | 75 | 100 | 50 | None. | None. | ..... | ..... | ..... | ..... | --- | --- |
| | Millimeters | 29 | 35 | 6 | ..... | ..... | ..... | ..... | ..... | ..... | --- | --- |
| 21.1° C. Tangential | Per cent | 50 | None | None. | None. | None. | ..... | ..... | ..... | ..... | --- | --- |
| | Millimeters | 6 | ..... | ..... | ..... | ..... | ..... | ..... | ..... | ..... | --- | --- |

In the diagrams (figs. 2 to 4) the data on median and tangential infections are treated together, because at temperatures below 10° C. there was no evidence of a difference in susceptibility to infection between the two positions. The total numbers of median and tangential infections by each pathogene for all temperatures and intervals are shown in Table 12, which also gives an index of the relative virulence of the four species of Fusarium under these conditions and of the resistance to infection of the six varieties.

TABLE 12.—*Total number of infections by four species of Fusarium on median and tangential cuts of six potato varieties at all temperatures and at all intervals*

[The maximum number possible in each square is 160]

| Culture | Position of cut | Russet Rural | White Rural | Green Mountain | Spalding Rose | Irish Cobbler | Triumph | Total |
|---|---|---|---|---|---|---|---|---|
| F. sulphureum | Median | 115 | 121 | 104 | 86 | 64 | 78 | 568 |
| | Tangential | 78 | 103 | 92 | 85 | 63 | 97 | 518 |
| F. coeruleum | Median | 107 | [1] 124 | 82 | 58 | [1] 78 | [1] 70 | 519 |
| | Tangential | 85 | [1] 102 | 70 | 71 | [1] 79 | [1] 87 | 494 |
| F. oxysporum | Median | 54 | 84 | 16 | 10 | 21 | 21 | 206 |
| | Tangential | 59 | 67 | 8 | 6 | 21 | 38 | 199 |
| F. trichothecioides | Median | 12 | 12 | 4 | 2 | 5 | 5 | 40 |
| | Tangential | 15 | 7 | 6 | 3 | 8 | 12 | 51 |
| Total | | 525 | 620 | 382 | 321 | 339 | 408 | 2,595 |

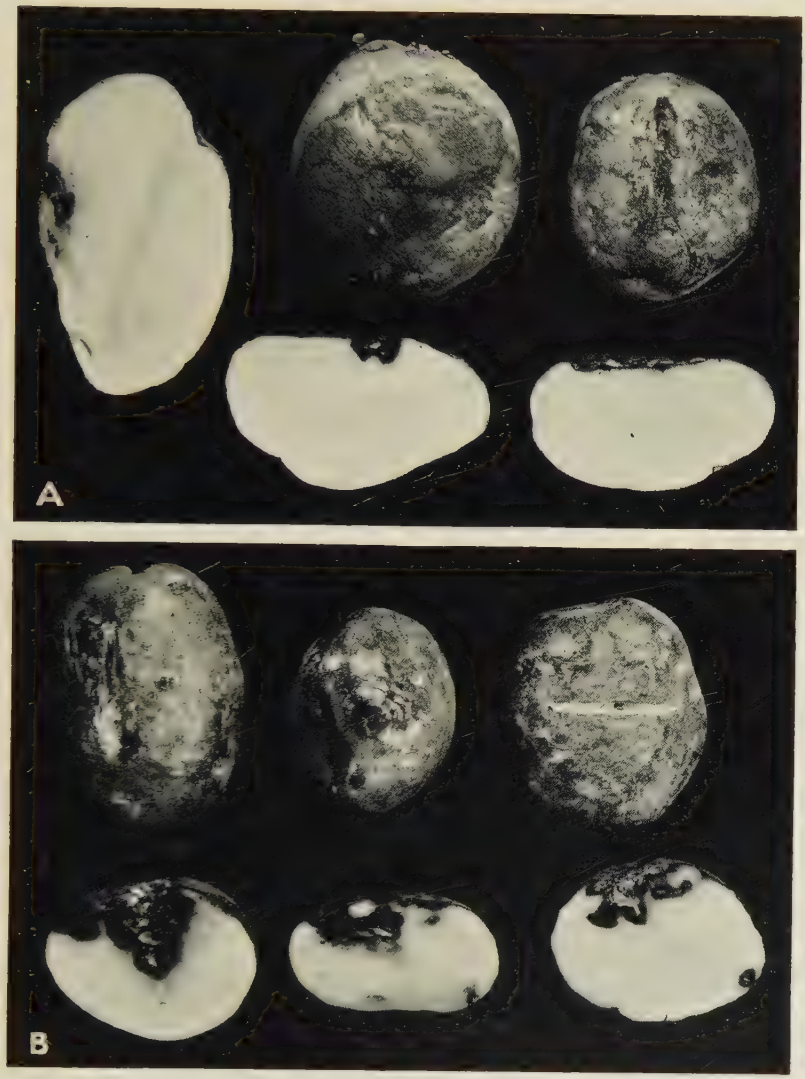
[1] Possible total of 156 instead of 160.

It may readily be seen that at temperatures below 10° C. (50° F.), even at favorable humidity, none of these varieties is able to form within 10 days a protective layer over or beneath wounds that excludes the more virulent storage-rot organisms. (Pl. 4.) Since experimental evidence has already been presented showing that at least two species of Fusarium may initiate infection at the lowest temperature at which potatoes can be stored safely and that low humidity neither prevents infection nor retards the progress of rot, it is likely that where wounds are numerous and contamination copious rot infection may be severe, even under storage conditions regarded as very favorable. It is not to be expected, however, that in nature virulent organisms will often be present in any such form or quantity as in these artificial inoculations.

To obtain evidence on the practical aspect, a further experiment involving different kinds of injuries, simulating those which occur in harvesting, was carried out. Tubers of the Russet Rural variety were skinned, cut, or bruised as before, but were inoculated with Fusarium cultures on soil or steamed wheat. The soil was a medium loam such as is used for potting plants, and it had been autoclaved for two hours. The cultures had been kept on soil for more than two months before their use in this experiment and were of tested virulence. At this time the original scanty growth of mycelium had nearly disappeared, and the soil was approaching air dryness. For inoculating it was mixed with water to form a thin mud in which the bruised or cut tubers were rubbed. (Pl. 5.) The grain cultures were intended to simulate contamination occurring in the field from vegetable débris. All the species grew well on this medium. In use a contaminated grain was inserted with forceps into a cut. The spore suspensions were managed as heretofore described.

After cutting and again after inoculation the tubers were divided into two lots and stored in the main cellar, one lot exposed to liberal ventilation, the other inclosed in a tightly-built, covered wooden box. The temperature varied from about 4° to 11° C., being slightly more equable in the box, and the humidity ranged from about 75 to 85 per cent and was generally higher in the box. The results are assembled in Table 13.

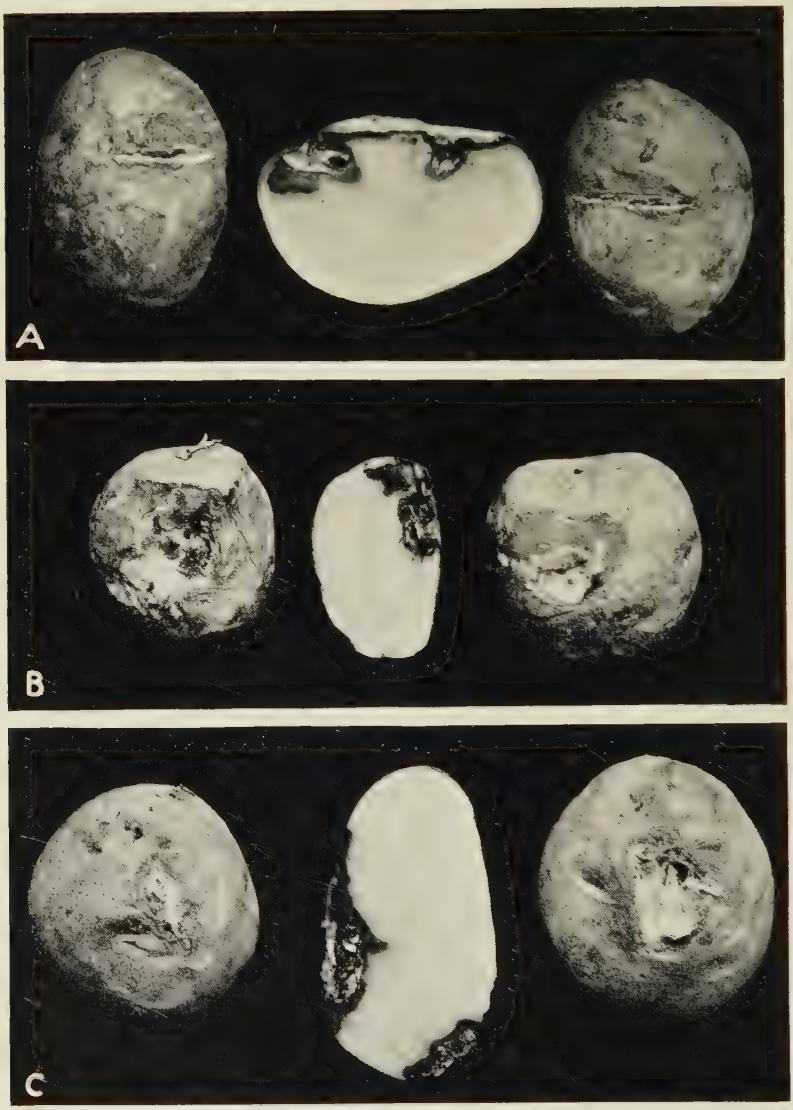
In general, previous conclusions as to the length of time ordinary field injuries under these storage conditions may remain susceptible to Fusarium infection are substantiated. As was to be expected, the amount of infection was less when a culture medium less favorable for growth of Fusarium than nutrient agar was used. Some infections classed as slight were apparently occluded by cork formation, others were evidently active. To classify them would have been speculative, and the observation has been frequently made that infections which are apparently latent while the temperature remains low often become active when the temperature is raised. The significant feature is the high proportion of infection in 3-day-old injuries when they are wet, as in inoculation with a spore suspension. (Pl. 6.) The conclusion may be reaffirmed that if the surface of potatoes is wet when they are placed in storage, or if it becomes so at any time within 3 to 10 days, depending on the temperature, infection of injuries is likely to occur, and once initiated infection is not easy to suppress by any sort of subsequent storage.




EFFECT OF INOCULATING POTATOES IN BRUISES

A, Russet Rural potatoes inoculated in bruises with a soil culture of *Fusarium coeruleum*; left, at once; middle, after 1 day; right, after 3 days. Infection is limited to inoculations made at once and after 1 day.

B, Russet Rural potatoes inoculated with germinating spores of *Fusarium sulphureum* 1 day after injuring the tubers. Left, bruised; middle, skinned; right, cut. Temperature, about 5° C.




INFECTION OF RUSSET RURAL POTATOES BY GERMINATING SPORES OF FUSARIUM SULPHUREUM 3 DAYS AFTER INJURING THE TUBERS

A, cut; B, skinned; C, bruised. Temperature about 5° C.

TABLE 13.—*Effect of kind of inoculum, character of injury, and storage conditions on infection of wounds of Russet Rural potato tubers by three species of Fusarium*

Explanation: *= *F. trichothecioides* substituted for *F. sulphureum*; ⊙=negative; ①=slight; ②=moderate ③=severe; ④=missing]

| Inoculum | Interval (days) | Cellar storage | | | | | | Closed-box storage | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | F. coeruleum | | | F. sulphureum | | | F. coeruleum | | | F. sulphureum | | |
| | | Skinned | Cut | Bruised | Skinned | Cut | Bruised | Skinned | Cut | Bruised | Skinned | Cut | Bruised |
| Soil culture | 0 | | | 3①<br>2⊙ | | | *2①<br>*3⊙ | | | 3①<br>2② | | | *5⊙ |
| | 1 | | | 3①<br>1②<br>6⊙ | | | *5①<br>*5⊙ | | | 8①<br>2② | | | 3①<br>7⊙ |
| | 3 | | | 10⊙ | | | *10⊙ | | | 2①<br>8⊙ | | | *10⊙ |
| Grain culture | 0 | | 5⊙ | | | 5③ | | | | 1①<br>1②<br>3⊙ | | 2①<br>1②<br>2③ | |
| | 1 | | 1①<br>9⊙ | | | 6②<br>3③<br>1⊙ | | | | 4①<br>6⊙ | | 5①<br>1③<br>4⊙ | |
| | 3 | | 1①<br>9⊙ | | | 5②<br>5③ | | | | 2①<br>8⊙ | | 4①<br>1②<br>4③<br>1⊙ | |
| Spore suspension | 0 | 5⊙ | 1①<br>4⊙ | 2①<br>3⊙ | 2②<br>1③<br>2⊙ | 2②<br>3③ | 1③<br>4③ | 5⊙ | 3①<br>2② | 3①<br>2⊙ | 2①<br>2③<br>1⊙ | 5⊙ | 5⊙ |
| | 1 | 10⊙ | 10⊙ | 10⊙ | 3①<br>1③<br>3③<br>3⊙ | 5①<br>3②<br>1③<br>1⊙ | 1①<br>4③<br>4③<br>1④ | 10⊙ | 10⊙ | 2①<br>8⊙ | 5⊙ | 2①<br>3②<br>2③<br>3⊙ | 3①<br>2②<br>5③ |
| | 3 | 10⊙ | 10⊙ | 10⊙ | 3①<br>1③<br>6⊙ | 2①<br>1②<br>2③<br>5⊙ | 3①<br>3②<br>4③ | 10⊙ | 10⊙ | 13⊙ | 1①<br>9⊙ | 2①<br>3②<br>5⊙ | 2①<br>2②<br>3③<br>3⊙ |

## EFFECT OF VARIETAL DIFFERENCE

The data presented suggest that differences in the amount of rot occurring in these six varieties are due more to the relative efficiency with which infection is excluded than to differential susceptibility of the tissue to disintegration once rot is established. The Rural New Yorker, whether of the smooth or russet-skinned type, shows a higher proportion of infection at each interval than the other varieties. In each variety, however, deep penetration occurs in individual instances, showing that they are not really resistant to decay. That varieties differ greatly in the rate at which they form suberin in injured tissues or lay down a wound periderm has been remarked by Appel (*1*) and by Priestley (*24*). The data herein presented indicate that these varieties may be arranged approximately in order of increasing susceptibility to wound rot infection as follows: Spaulding Rose, Irish Cobbler, Green Mountain, Triumph, Russet Rural, and White Rural. The results of histological studies show that about the same order is followed in the rate of healing wounds, the Rural varieties being the slowest. Rapid suberization of injuries is a character that might well be sought in the production of new varieties, and the performance in this respect should be known before a new seedling is considered worthy of introduction.

### RELATION OF RELATIVE HUMIDITY AT HIGHER TEMPERATURES TO INFECTION

The experiments thus far considered were all carried out at temperatures representative of practical storage conditions, mostly about 6.7° C. (44° F.) The absence of a marked influence of humidity on infection has been noted and a hypothesis offered in explanation thereof. It is pertinent to inquire whether the absence of a significant effect of humidity is due to the experimental method employed—that is, are differences in atmospheric humidity largely neutralized by the use of agar cultures or spore suspensions for inoculation, or is it due to the lesser change in evaporating power of the air with a given change in humidity at low temperatures than occurs at higher temperatures? To determine this, further experiments were carried out along the same line. Temperatures of 12° and 23° C. (53.6° and 73.4° F.) were employed to simulate the moderately cool or warm conditions in which potatoes are sometimes placed during storage or transit.

It would have been desirable to arrange two parallel sets of conditions employing the same saturation deficits at the two temperatures. It happened that among the experimental infection chambers at the cold-storage laboratory of the Department of Agriculture at the Arlington Experiment Farm, Rosslyn, Va., there were four chambers already in operation at each of these temperatures which provided a range of humidity from about 50 per cent to nearly saturation.

TABLE 14.—*Relation of four relative humidities at two temperatures to infection of Russet Rural by five species of Fusarium, showing the percentage of infection and the average penetration in millimeters*

[Symbols: S=saturation deficit (mm. Hg); H=relative humidity (per cent)]

| Fusarium species and inoculum | Temperature 12° C. | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| | S 0.9, H 90 | | S 2.4, H 78 | | S 3.6, H 67 | | S 4.0, H 61 | |
| | *P. ct.* | *Mm.* | *P. ct.* | *Mm.* | *P. ct.* | *Mm.* | *P. ct.* | *Mm.* |
| F. trichothecioides—Spores | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| F. trichothecioides—Mycelium | 50 | 2 | 50 | 3 | 50 | 2 | 25 | 2 |
| F. sulphureum—Spores | 25 | 2 | 25 | 3 | 0 | 0 | 50 | 3 |
| F. sulphureum—Mycelium | 100 | 7 | 75 | 5 | 25 | 5 | 75 | 3 |
| F. coeruleum—Spores | 0 | 0 | 0 | 0 | 0 | 0 | 50 | 2 |
| F. coeruleum—Mycelium | 100 | 4 | 100 | 1 | 100 | 1 | 100 | 2 |

| Fusarium species and inoculum | Temperature 23° C. | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| | S 1.6, H 92 | | S 4.6, H 76 | | S 7.5, H 63 | | S 11.8, H 42 | |
| | *P. ct.* | *Mm.* | *P. ct.* | *Mm.* | *P. ct.* | *Mm.* | *P. ct.* | *Mm.* |
| F. trichothecioides—Spores | 0 | 0 | 25 | 8 | 0 | 0 | 0 | 0 |
| F. trichothecioides—Mycelium | 50 | 14 | 25 | 12 | 100 | 6 | 50 | 3 |
| F. sulphureum—Spores | 75 | 13 | 0 | 0 | 50 | 4 | 25 | 2 |
| F. sulphureum—Mycelium | 75 | 14 | 75 | 14 | 100 | 5 | 75 | 7 |
| F. coeruleum—Spores | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| F. coeruleum—Mycelium | 100 | 6 | 100 | 8 | 100 | 8 | 75 | 5 |
| F. radicicola—Spores | 0 | 0 | 0 | 0 | 0 | 0 | 25 | 2 |
| F. radicicola—Mycelium | 75 | 11 | 100 | 12 | 75 | 3 | 100 | 3 |
| F. oxysporum—Spores | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| F. oxysporum—Mycelium | 75 | 9 | 100 | 7 | 50 | 12 | 75 | 5 |

In these chambers, which are of about 1 cubic meter capacity, the humidity is controlled by the use of brine pans over which air slowly circulates, but the temperature control is thermostatic. The same experimental methods as heretofore described were followed throughout. Two varieties of potatoes, Russet Rural and Triumph, were used, and to the three species of Fusarium, *F. trichothecioides*, *F. sulphureum*, and *F. coeruleum*, previously included, *F. radicicola* and *F. oxysporum* were added at the higher temperatures. Both mycelium and spore inoculations were made, the incubation period being three weeks. The results with Russet Rural appear in Table 14. Those with Triumph were so nearly the same that they will be mentioned only in the discussion.

For the three species used at both temperatures the percentage of infection is not greater at one temperature than at the other, but the depth of penetration is of course greater at the higher temperature. At 12° C. there is no significant difference either in percentage of infection or in depth of penetration within the humidity range of 90 to 61 per cent. At 23° there is a slight falling off in percentage of infection from 92 to 42 per cent humidity and the decline was greater in Triumph than in Russet Rural. There is a corresponding decrease in depth of penetration, and this is more marked in Russet Rural than in Triumph. The differences though not great are consistent. The incubation period in this test was short, and sound conclusions as to the real extent and severity of infection could hardly be drawn.

Before repeating the experiment with a longer term, an attempt was made to regulate the humidity in the four chambers at 23° C. so as to provide the same series of saturation deficits as were maintained at 12°. Owing to the lack of close control, the average relative humidities that were actually maintained differed somewhat from those desired, and the saturation deficits in the two temperature series were only approximately alike. Only one variety, Green Mountain, was used, and the experiment continued for eight weeks, though notes on infection also were made after three weeks. The most striking feature of the results after eight weeks, as compared with the shorter term, was the aggressive development of some of the spore infections, which showed only shallow discolored pits at the end of three weeks. This was particularly the case in tubers inoculated with *Fusarium oxysporum*. Upon cutting the tubers after eight weeks, it was found that spore infections in this species had entered the vascular bundles and spread widely, passing out into the cortical parenchyma and causing general decay. Infections of this type obviously were not related in position to the point of inoculation and hence were not affected by the normal wound-healing process in the parenchyma.

Leach (*10*) has recently called attention to the establishment of the potato blackleg organism in the vascular system and its persistence there until environmental conditions and the depletion of starch in the tuber enable it to initiate generalized decay. The present observation that *Fusarium oxysporum* also may be inoculated into the vascular system of the tuber through mechanical injuries, in addition to its known capacity to invade through the stolons, is of interest in the bearing on the rather frequent decay in transit of southern potatoes, which is traceable to vascular Fusaria.

The results after eight weeks are assembled in Table 15.

TABLE 15.—*Relation of four relative humidities at two temperatures to infection of potatoes by six species of Fusarium, showing the percentage of infection and the average penetration (millimeters)*

[Symbols: S=saturation deficit (mm. hg); H=relative humidity (per cent)]

| Fusarium species and inoculum | | Temperature, 12° C | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| | | S 1.8, H 85 | | S 2.6, H 78 | | S 4.1, H 61 | | S 5.2, H 51 | |
| | | *P. ct.* | *Mm.* | *P. ct.* | *Mm.* | *P. ct.* | *Mm.* | *P. ct.* | *Mm.* |
| F. trichothecioides | Spores | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| | Mycelium | 0 | 0 | 50 | 3 | 100 | 10 | 50 | 8 |
| F. sulphureum | Spores | 67 | 3 | 100 | 2 | 100 | 13 | 100 | 12 |
| | Mycelium | 100 | 26 | 100 | 11 | 100 | 12 | 100 | 20 |
| F. coeruleum | Spores | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| | Mycelium | 100 | 7 | 100 | 13 | 100 | 10 | 100 | 12 |
| F. radicicola | Spores | | | | | | | | |
| | Mycelium | | | | | | | | |
| F. eumartii | Spores | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| | Mycelium | 52 | 2 | 0 | 0 | 0 | 0 | 0 | 0 |

| Fusarium species and inoculum | | Temperature 23° C. | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| | | S 1.1, H 94 | | S 2.3, H 89 | | S 4.4, H 80 | | S 5.0, H 75 | |
| | | *P. ct.* | *Mm.* | *P. ct.* | *Mm.* | *P. ct.* | *Mm.* | *P. ct.* | *Mm.* |
| F. trichothecioides | Spores | 17 | 8 | 0 | 0 | 0 | 0 | 0 | 0 |
| | Mycelium | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| F sulphureum | Spores | 33 | 20 | 20 | 15 | 0 | 0 | 100 | 19 |
| | Mycelium | 50 | 16 | 50 | 9 | 50 | 21 | 50 | 3 |
| F. coeruleum | Spores | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| | Mycelium | 75 | 10 | 100 | 11 | 100 | 17 | 100 | 15 |
| F. radicicola | Spores | 20 | 27 | 67 | 22 | 40 | 16 | 33 | 6 |
| | Mycelium | 25 | 8 | 50 | 4 | 0 | 0 | 50 | 3 |
| F. eumartii | Spores | 60 | 22 | 40 | 13 | 100 | 14 | 0 | 0 |
| | Mycelium | 75 | 16 | 75 | 9 | 100 | 17 | 75 | 10 |
| F. oxysporum | Spores | 80 | 27 | 17 | 6 | 100 | 22 | 71 | 9 |
| | Mycelium | 75 | 27 | 75 | 11 | 50 | 18 | 75 | 14 |

All instances of penetration less than 2 mm. are treated as negative. It is to be noted that the percentage of infection and the depth of penetration at 12° C. are about the same at each humidity, whereas at 23° there is a slight decrease only in penetration with diminishing humidity. Infections from spore inoculations are somewhat sporadic, but occur at least as frequently at low humidity as at high—further evidence that the effect of humidity is largely neutralized by this method of inoculation and that infection is dependent on defects in the tuber's healing process. So far as practical control of infection or decay is concerned, it is evident that reduction of humidity to 80 per cent, even at a temperature so unfavorably high for potato storage as 22.7° C. (73° F.), is not of great avail. This relative humidity has about the same effect in respect to the evaporating power of the air as 62 per cent humidity at 11° C. (54° F.), and 45 per cent humidity at 6.7° C. (44° F.). At either temperature such humidity would be not only difficult to attain under practical storage conditions, but would result in marked shriveling. It may be emphasized again that the temporary presence of a water film is the effective factor in infection. If potatoes are to be stored

free from risk of wound rots the injuries received during harvesting operations must be thoroughly dried before the tubers are placed in storage.

## DISCUSSION OF RESULTS

### PRESTORAGE HANDLING METHODS TO PREVENT INFECTION THROUGH HARVESTING INJURIES

From the experimental results and the comments thus far presented, it may be readily seen that the prestorage treatment of potatoes should aim to attain three principal results: (1) A minimum of mechanical injuries; (2) prompt and thorough drying; (3) in the case of somewhat immature stock, to allow an interval for curing before exposure to the handling and close packing incident to bulk storage. When the temperature of the storage house is below 10° C. (50° F.) there will be less risk of wound rot developing if the tubers are not placed directly in storage but are kept under shelter at any practicable higher temperature for a period of several days.

In the reduction of mechanical injury, proper manipulation of the digger is one of the principal factors. Many growers are recognizing the importance of moving a liberal quantity of soil with the tubers to protect them from bruising and are making adjustments to their machines so as to minimize cuts, for example, by covering with rubber or burlap the forks, shakers, or other sharp edges and corners against which the tubers are thrown. Where weather conditions during harvesting are favorable to infection of wounds, any method that results in fewer injuries will afford a corresponding gain in the keeping quality of the crop. That wounds greatly facilitate not only Fusarium rot but also late-blight rot infection was shown by Murphy and McKay (*17*) and by Löhnis (*13*). Wounds are the principal source also of the wet rot caused by Pythium (*8*). When the importance of injuries as predisposing to storage rot is fully realized, other methods will suggest themselves for eliminating the unnecessarily rough handling too often given potatoes.

Even though tubers are dry when first placed in storage, under certain conditions later they may become covered with moisture, a process often described as sweating. This may be due to the initially high rates of respiration and transpiration of freshly dug tubers continuing high for some time in storage, or it may arise during the storage term when, as a result of close piling in large masses, the removal of the heat and moisture of respiration is restricted and the atmosphere within the mass assumes a higher temperature than that of the storage room. The ascending current of warm air is cooled by contact with the air above the bin, with the result that moisture is deposited in the upper layers. This cause of sweating was demonstrated in investigations at the Marble Laboratory (*18*), and it was also shown that sweating, particularly if it is continuous, is associated with early sprouting. Both sweating and premature sprouting are favorable to wound infection and rapid progress of decay. To prevent sweating it is necessary to prevent rise of temperature within the bin above that of the storage chamber. This is particularly important from the standpoint of controlling wound infections during the first few weeks of storage, but it must be remembered that Fusarium rot may originate in other lesions than those caused

mechanically, so that maintenance of the stock in dry condition throughout is always to be desired.

In tubers that are not fully mature the cork cambium may be still active or not fully suberized, and it readily gives way when the tubers are knocked together, resulting in skinning and bruising. When exposed to drying, even for a few days, the skin hardens, probably through simple dehydration, the cambium ceases activity, and the youngest periderm cells become suberized. The skin thus rapidly becomes increasingly protective against mechanical injury, and the tubers may be handled safely in bulk.

With properly matured stock and under favorable weather conditions it is not difficult to meet these requirements, and the fact that they are ordinarily well satisfied is shown by the small proportion of wound rot in the crop aggregate. It is in the exceptional circumstances attendant on harvesting a relatively immature crop, as in some northern seed localities, or when digging must be done in continuous wet weather, that special provision is required chiefly in respect to drying and curing the stock. Both requirements are fully met by picking directly into slatted crates or similar ventilated containers and storing the crop temporarily under cover from rain, where ample ventilation may be provided. The success of this method has been demonstrated in at least one instance in Pennsylvania, where a grower, despite very unfavorable harvesting weather, preserved a crop of about 2,300 bushels practically free from rot, though in previous years, with better digging conditions, much loss in storage had occurred.

For the storage of seed potatoes, particularly where only a poorly ventilated, inadequately cooled storage house is available, the application of a disinfectant at digging time has been advocated. Since seed potatoes are ordinarily disinfected before planting to eliminate superficial tuber-borne diseases, a treatment applied at harvest time might be made to serve a double purpose. Pratt's (*23*) experiments showed that potatoes could be protected very effectively against dry rot caused by *Fusarium trichothecioides* by dipping for two hours in either formaldehyde or mercuric chloride of standard strength as used in seed-potato treatment, provided the application were made within 48 hours after digging. Even badly bruised tubers kept without decay after this treatment. The mercury treatment after longer intervals was slightly more effective than formaldehyde, but neither lime nor sulphur applied as a dust afforded protection in deep bruises. It is to be noted that disinfection in this way is recommended only where poor storage facilities must be utilized, and obviously no form of disinfection can be employed on stock destined for food.

Though prestorage disinfection of potatoes has but limited practical application, a thorough annual cleaning of the storage cellar and periodic disinfection, particularly if storage rot has been prevalent in previous crops, are always to be advised. Pethybridge (*20*) demonstrated the presence of virulent Fusarium spores on the walls and floors and in the air of potato-storage rooms. For disinfection either an antiseptic wash or fumigation may be employed. Copper sulphate or formaldehyde in a 1 to 2 per cent solution effectively serves this purpose, and is preferably applied as a spray. Fumigation may be carried out according to the standard procedure, using 3

pints of formaldehyde and 23 ounces of potassium permanganate for each 1,000 feet of volume to generate the gas, and the room should be kept tightly closed for at least 24 hours.

### STORAGE METHODS TO INSURE KEEPING QUALITY AND PREVENT ROT

The full storage term of potatoes is sometimes differentiated into early, middle, and late periods corresponding to three roughly distinguishable stages in the vital cycle of the tuber. In the early period respiratory activity is initially high but declining, the periderm is at first relatively delicate but soon toughens, and sprouting does not occur even at favorable temperature. The storage requirements during this period have been summarized as (1) maintenance of dry stock, (2) prevention of heating. During the middle period the tubers are profoundly dormant, respiratory activity is low, the skin has become firm and tough, and sprouting is still in abeyance. If proper storage conditions have been provided during the early period, so that the stock is dry and free from internal heat, dormancy may be maintained during an acceptably long middle period with only moderately low temperature, 4° to 7° C. (40–45° F.), though there is no objection to lower, and with a minimum provision for ventilation. In the third period the innate dormancy terminates, and prevention of sprouting depends on the imposition of an unfavorably low temperature.

Coincident with the breaking of the rest period the respiration rate rises again. Investigations at the Marble Laboratory (*18*) showed that if the storage temperature is above 3° to 4° C. (38–40° F.) rise of temperature due to accumulated products of respiration can not be prevented in deep bins, 6 to 8 feet, but can be overcome only by the use of small packages, such as crates or bags, piled so as to permit air circulation all around. As the temperature rises within the bin, sprouting is further accelerated, and sweating is likely to occur. The attempt to retard germination by lowering the temperature of the storage room at this time only increases the tendency to sweat. The combined effect of rise of temperature, sweating, and germination is to favor the progress of incipient decay and the occurrence of fresh infections through the sprouts.

The prevention of decay during late storage is very closely related to the suppression of germination, and both are dependent largely on proper handling during the early period. The prevention of decay is also dependent on the prestorage handling.

The fundamentals of potato storage as at present understood, with regard for both the prevention of decay and the maintenance of dormancy, may now be stated. The first three conditions are the outgrowth of the present study, the remainder are the recommendations of the Pennsylvania Committee on Potato Storage, as embodied in a report of the Marble Laboratory (*18*).

## CONCLUSIONS

Potatoes should be dug and handled throughout all storage and transit operations in such a manner as to cause a minimum of cuts and bruises. Even minute skin abrasions may become the seat of fungous infection.

As promptly as possible after digging, the tubers must be superficially dried, though this should be done without exposure to excessive sunlight or heat. The surface must remain dry for at least several weeks after they are placed in storage and preferably should be so throughout the term.

If the tubers have not fully ripened in the ground, they should not be handled after picking until sufficient time has elapsed for the skin to harden as well as dry; this is hastened by thorough ventilation.

The temperature of the storage is the controlling factor in determining the storage conditions necessary for delaying germination.

When the storage temperature is low, from 30° to 35° F., the heat of respiration is so slight that bin storage may be employed with satisfactory results.

When, however, a storage temperature of 38° to 40° F. is employed, bin storage is apt to result in early germination.

Ventilation is not effective in delaying germination in deep bin storage.

With a storage temperature of 38° to 40° F. storage in small packages with opportunity for the escape of the products of respiration on all sides of the package is desirable. Crates or bags piled with ample dunnage comply with these requirements.

Ventilation is the most effective agency for removing the products of respiration. It should be employed in sufficient measure to do this promptly and completely.

When the storage temperature is 38° to 40° F., crate or bag storage with ventilation supplies the proper holding conditions for delaying germination until the end of the storage term.

## SUMMARY

Terminal market inspection reports from 17 States producing a surplus of late potatoes indicate the occurrence of an average of 4 per cent loss due to Fusarium rot. In individual shipments there is sometimes 50 per cent or more of this rot.

Since these reports concern stock that in most cases has previously been graded, it is believed that the total loss from Fusarium rot is from 5 to 10 per cent of the annual crop. Occasional losses for individual States up to 25 per cent have been reported to the Plant Disease Survey.

Various types of handling injuries, including cuts, bruises, and skin abrasions, are the source of Fusarium rot about twice as often as any other source, including the late-blight lesions and frost injury.

The species of Fusarium which most frequently cause rot in storage potatoes are *F. coeruleum*, *F. sulphureum*, and *F. trichothecioides*. The latter is prevailingly western in distribution, though infected potatoes of western origin have been found in eastern markets. The other two species are northern in range, and *F. coeruleum* at least has been reported from eastern Canada and New England to the Pacific coast.

*Fusarium eumartii*, *F. radicicola*, and *F. oxysporum*, all vigorously pathogenic to potatoes at higher temperatures, can initiate only slight and transitory infection at the temperatures that prevail in potato storage, i. e., below 10° C. (50° F.)

*Fusarium sulphureum* and *F. coeruleum* are able to initiate infection and cause progressive decay down to nearly the lowest temperature that may safely be employed in potato storage.

No marked difference in susceptibility to infection or in rate of decay was found between mature recently dug potatoes and those which were kept in storage conditions that maintained dormancy up to the end of April.

At a representative storage temperature, 6.7° C. (44° F.), there was no marked difference in the amount of infection or the progress of decay within a range of constantly maintained humidities from 70 to 95 per cent of saturation, and infection was independent also of the rate of air exchange between practically still air and a complete change four times an hour. At this temperature *Fusarium coeruleum* can initiate infection at 50 per cent relative humidity. Essentially similar results were obtained from inoculations with agar cultures and spore suspensions in water.

The absence of any effect due to humidity is attributed partly to the fact that either form of inoculum establishes its own hygroscopic relations, which are maintained until altered by the evaporating power of the air. At the temperatures that prevail in potato storage the difference in evaporating power between 50 and 95 per cent relative humidity does not suffice to reduce the moisture content of the inoculum or superficial tissue of the host below the minimum required by the pathogene before penetration occurs.

At the same temperature, 6.7° C., it was also found that infection was not materially affected when the cut surface was inoculated at once while still moist or was allowed to dry for 2 to 72 hours before inoculating.

The direct effects of the environmental factors—temperature, humidity, and rate of air exchanged—on the growth of the pathogene are overshadowed by the effect of temperature on the wound-healing processes—suberization and wound-periderm formation—of the potato tuber. Suberization alone of the cell walls within and adjacent to the cut does not suffice to exclude pathogenes of this type; at 6.7° C. wound-periderm formation is so greatly delayed that in the absence of a direct environmental effect there is no obstacle to infection.

The rate of healing of cuts was studied in six varieties of potatoes at six temperatures throughout 10 days; also the relation of healing to infection by four species of Fusarium. A marked difference in the rate of healing occurs between such varieties as Rural New Yorker, in which the process is slow, and Irish Cobbler or Spaulding Rose, in which it is rapid.

In the Rural New Yorker variety approximately the following intervals at the temperatures stated are required for the production of a wound periderm that can exclude *Fusarium coeruleum* and *F. sulphureum*: 21° C. (70° F.), 3 or 4 days; 15.5° C. (60° F.), 5 or 6 days; 10° C. (50° F.), more than 8 days; below 10° C., more than 10 days. In Spaulding Rose from 1 to 3 days suffices at 21° and 15.5°, but 10 days are not sufficient at temperatures below 10° C.

At temperatures which permit of fairly rapid healing there is still no limiting effect of humidity, within the ordinary range, on infection by Fusarium, whether mycelium or a spore suspension is used to inoculate; though as the temperature is raised, the effect of low humidity becomes more marked. At 23° C. (74° F.), for example,

infection readily occurs from either type of inoculation at 80 per cent humidity. In the effect on the evaporating power of the air this is equivalent to reducing the humidity at 6.7° C. to 45 per cent.

It is concluded that the presence of moisture in the wound and its persistence there until infection has occurred greatly overshadows, in its influence on infection, the relative humidity of the atmosphere.

Wound infection and the ensuing rot in storage can not be prevented or controlled simply by manipulation of the temperature and humidity of the storage room. Prevention consists essentially in careful handling to reduce mechanical injury to the minimum. Control consists fundamentally in removing superficial moisture from the tubers as promptly as possible after digging and keeping the stock dry during at least the first four weeks of storage. So long as the stock is kept dry, the humidity should be that most favorable for maintaining the quality of the tubers, in general the higher the better. If the tubers are stored in small packages, as slatted crates or bags piled with suitable dunnage, so as to provide thorough ventilation through and around the pack, the temperature need not be lower than 4.4° to 7° C. (40–45° F.) for either the prevention of Fusarium rot or the maintenance of dormancy.

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